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Report on Understory Response to Different Prescribed Fire Intensities

RMRS-99156-RJVA

Final Report

REPORT ON UNDERSTORY RESPONSE TO DIFFERENT PRESCRIBED FIRE INTENSITIES

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EXECUTIVE SUMMARY

This report is the final report for Research Joint Venture Agreement No. RMRS-99156-RJVA, Understory response to different prescribed fire intensities in the urban/wildland interface around Flagstaff, Arizona. The report is divided into two parts. In part one, we present results that have been submitted to peer-reviewed journals. In part two, we have listed all the publications and presentations based upon the research funded by Research Joint Venture Agreement No. RMRS-99156-RJVA. Also included in this report is a copy of the dissertation, "Understory Plant Community Dynamics in Southwestern Ponderosa Pine Forest Restoration" by Julie Korb.

Summary of Major Findings

This research has direct implications for lay people, scientists, and land managers who are involved in ponderosa pine restoration projects in the Southwest. This research can be integrated into ponderosa pine forest adaptive ecosystem management. Our research investigated different aspects of understory plant community dynamics in southwestern ponderosa pine forests. Any of the land management recommendations from this research should be placed in the context of the particular restoration treatment in which it is being applied. Ponderosa pine restoration is an evolving field that incorporates a diversity of individual interests from people who are trying to put theory and knowledge into practice. The results from this research need to be balanced with the practicality of their applicability in different management situations (e.g., availability of funding, personnel, project goals, etc.). Therefore, these results do not represent a final answer to the questions proposed but rather a base of knowledge in which discussions can begin.

Research Project #1

Our first objective of this research was to determine whether different understory plant monitoring sampling techniques and sampling sizes would result in inconsistent data and if this would influence the ability to detect change in ponderosa pine restoration treatments. Our results illustrated that the sampling technique chosen for monitoring herbaceous and shrub species richness and foliar cover in restoration studies can greatly influence the ability to detect change. Specifically, the results from our research showed that large area sampling techniques were the most effective at capturing species richness and rare and exotic species. Modified-Whittaker plots returned on average the highest species richness in all sampling technique comparisons and captured the most rare and exotic species. In comparison, point-intercept transects captured the fewest species. When choosing a sampling technique, decisions must be made about plot size and shape, the parameters to be measured, and the frequency, precision and location of measurements (Stohlgren 1994). Reference conditions are often cited as the goal for restoration treatments. This study illustrates that the type of sampling technique used to determine reference conditions should be similar to the sampling technique used to monitor change or the data may lead to inaccuracy, confusion, or apparent over-achievement of goals.

Research Project #2

A second objective of this research was to quantify the effect of restoration thinning alone and thinning and prescribed burning on arbuscular mycorrhizae (AM) and ectomycorrhizae (EM) fungal propagule densities and assess the relationships between

mycorrhizal fungal propagule densities and plant community properties in southwestern ponderosa pine forests. Our results indicated that population densities of AM fungi can rapidly increase following restoration thinning alone and thinning and prescribed burning. The relative amount of infective propagules of AM fungi was significantly negatively correlated with overstory tree canopy cover and litter cover and positively correlated with herbaceous understory species richness and graminoid cover.

These results have application to land managers who are trying to increase herbaceous understory richness and abundance. Some evidence suggests that prior to the mid 1880's, ponderosa pine understory communities were dominated by warm-season (C_4) grasses, which are often strongly mycotrophic (Cooper 1960, Pearson et al. 1971,Wilson and Hartnett 1998). However, current ponderosa pine forests are dominated by species that often form no mycorrhizal associations (e.g., *Carex* spp.), or C_3 grasses that are often weakly mycotrophic (Wilson and Hartnett 1998). This community has been established because the natural fires that historically would minimize competition between ponderosa pine and herbaceous plants have been suppressed and shade-tolerant C_3 grasses are better adapted to these environments. Without the reduction of EM tree competition and reintroduction of fire, the understory of southwestern ponderosa pine forests will likely continue to be dominated by weakly nonmycotrophic *Carex* and weakly mycotrophic C_3 grasses. One can predict that increased populations of AM fungi in the thinned only and thinned and prescribed burned restoration stands may assist in the replacement of weakly mycotrophic species by strongly mycotrophic species, thereby increasing C_4 grass cover and leading to the maintenance of a stable sward of mycorrhizal compatible species (Francis and Read 1994, Johnson 1998). This has important implications for land managers trying to restore the herbaceous understory of these forests because most understory plants depend upon AM associations for normal growth. Future studies of AM in ponderosa pine restoration areas will require analysis of the species composition of the fungal communities to determine if a shift in the fungal community is occurring in response to restoration treatments and whether these shifts impact the plant community composition. Recent research in a variety of environments has shown that mycorrhizal interactions may be important determinants of plant diversity, ecosystem variability, and productivity (Hartnett and Wilson 1999, van der Heijden et al. 1998a, van der Heijden et al. 1998b, and Klironomos et al. 2000). Therefore, future studies in ponderosa pine restoration treatment areas are needed to more fully understand responses of AM fungal communities and assess feedbacks between AM fungal and plant communities.

Research Project # 3

A third objective of this research was to determine the effect slash pile burning on densities of plant and AM fungal propagules and soil physical and chemical properties and determine the effect of soil and seed amendments on the rate of native herbaceous plant establishment within burned slash pile scars. The results indicated that without amendments, the relative amount of AM fungal propagule densities, number of viable seeds in the soil seed bank, and extant vegetation were significantly lower and soil properties were significantly different outside than inside slash pile scars. Seed/soil amendments had significantly higher cover of native forb and graminoid species in comparison to the other treatments. In addition, the seed/soil amendments had higher plant density, cover, and height than the seed only amendments. These results illustrate

that adding both seed and living soil to slash pile scars can increase plant cover of desirable native forbs and grasses.

From these results we recommend land managers minimize burning large piles of slash that will result in severe soil heating, vegetation changes, and biotic and abiotic soil changes. Management decisions about slash removal need to take into consideration numerous factors such as the feasibility of other slash removal techniques including chipping and broadcast burning slash, the effects of these alternative techniques on ecosystem structure and function, and financial and personal constraints. Under scenarios where slash pile burning is the only realistic management option for reducing large amounts of fuel safely, we recommend that slash should be piled and burned on roads that are to be obliterated to minimize additional soil disturbance within the restoration treatment areas. We also recommend that severely burned slash pile scars should be treated with seed and soil amendments within the first growing season following burning to increase the rate of native plant establishment and discourage the invasion of exotic species. Native seeds of species common in the area should be used from a local source to minimize genetic contamination for seeding amendments and soil for the soil amendment treatments should be taken from stockpiled soil created during road building for the restoration treatments.

Research Project #4

A fourth objective of this research was conducted to quantify the effect of different harvest systems and thinning intensities on forest floor disturbance and short-term herbaceous vegetation responses in ponderosa pine forest restoration in northern Arizona. Tree thinning intensity did not significantly affect soil disturbance, dead woody biomass or herbaceous vegetation response. In contrast, the harvest system did affect these variables. The whole-tree system had the largest proportion of high soil disturbance (13%) and the lowest dead woody biomass (38.94 kg/ha) over the machine and hand harvest systems. The whole-tree system had a significant increase (14%) in the proportion of non-native herbaceous cover three years following the initial treatments, which was associated with soil profile disturbance; there were no significant differences for the machine or hand systems. These results suggest that the harvest system has a greater impact on forest soils and herbaceous vegetation than the intensity of tree removal, which has important implications for forest restoration because large numbers of trees are often removed to thin dense forest stands to emulate pre-settlement structure, thus indicating that high tree removal does not necessarily result in high soil disturbance.

We recommend that managers choosing a harvesting system for restoration should try to design treatments that will reduce unnecessary disturbance. Specifically, managers need to choose the harvesting system on a site-specific basis taking into account ecological components (e.g., soil type, soil texture, soil bulk density, soil moisture content at time of thinning), economical constraints (e.g., amount of money and time available to remove trees), and feasibility (e.g., type of mechanized equipment available). As a result, by including ecological components, which are not always included in the process of choosing harvesting systems, the outcome of the thinning treatment will be more compatible with restoration goals.

Findings Not Included in Report

Two research elements are not included in this report. First, we cannot report the overall response of the herbaceous vegetation to the experimental treatments because prescribed burning was initiated in different years for different blocks and therefore more post-treatment data needs to be collected before these data can be analyzed. In the summer of 2003, we will collect herbaceous vegetation data for all the study sites. This will be the 5th consecutive year of post-treatment data following the initial thinning treatments in all blocks. Data will be analyzed and a manuscript will be written and submitted to a peer-reviewed journal following the collection of these data. Second, the response of the soil seed bank to experimental treatments is not included in this report. Because of the timing differences in the prescribed burning treatments this study was not able to stand alone as a peer-reviewed publication. Instead, this research will be combined with soil seed bank studies conducted in other ponderosa pine research areas in northern Arizona (Mt. Trumbull and North Rim of the Grand Canyon) and will be written up as a peer-reviewed manuscript. We will provide copies of these manuscripts once they are completed and accepted for publication.

Conclusion

The cooperative work of Grand Canyon Forests Partnership and the USDA Forest Service in the Flagstaff urban/wildland interface gained national attention during the severe 2000 fire season, when the "Flagstaff Plan" was much debated by proponents and opponents. We hope that our data presented in this report will be helpful in explaining the effects of the experimental treatments on mycorrhizae, soil physical and chemical properties, and the herbaceous vegetation.

Literature Cited

Arnold, J. F. 1955. Changes in ponderosa pine bunchgrass ranges in northern Arizona resulting from pine regeneration and grazing. Journal of Forestry 48: 118-1266.

Buckner, D. L. 1985. Point-intercept sampling in revegetation studies: maximizing objectivity and repeatability. American Society for Surface Mining and Reclamation, Denver, Colorado.

Cooper C. F. 1960. Changes in vegetation, structure, and growth of southwestern pine forest since white settlement. Ecological Monographs 30: 129-164.

Dhillion S. S., and R. C. Anderson. 1993. Seasonal dynamics of dominant species of arbuscular mycorrhizae in burned and unburned sand prairies. Canadian Journal of Botany 71: 1625-1630.

Francis, R., and D. J. Read 1994. The contributions of mycorrhizal fungi to the determination of plant community structure. Plant and Soil 159: 11-25.

Hartnett, D. C., and G. W. T. Wilson. 1998. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. Ecology 80: 1187-1195.

Johnson, N. C. 1998. Responses of *Salosa kali* and *Panicum virgatum* to mycorrhizal fungi, phosphorus and soil organic matter: implications for reclamation. Journal of Applied Ecology 35: 86-94.

Klironomos J. N., J. McCune, M. Hart, and J. Neville. 2000. The influence of arbuscular mycorrhizae on the relationship between plant diversity and

productivity. Ecology Letters 3: 137-141.
Pearson, H. A., J. F. Mann, and D. A. Howard 1971. Timing use of cool- and warm season grasses on pine ranges. Journal of Range Management 24: 162-163.
Sackett S. S. 1984. Observations on natural regeneration in ponderosa pine following a prescribed fire in Arizona. USDA Forest Service Research Note RM-435
Stohlgren, T. J. 1994. Planning long-term vegetation studies at landscape scales in: Ecological Time Series (eds. Powell, T. and J. Steele), Chapman and Hall, New York, NY: 209-241.
Sutter, R. D. 1996. Monitoring, in: Restoring diversity—strategies for reintroduction of endangered plants (eds D. A. Falk, C. I. Millar, and M. Olwell), Island Press, Washington, D.C.: 235-264.
van der Heijden, M. G. A., T. Boller, A. Wiemken, I. R. Sanders. 1998a. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology 79: 2082-2091.
van der Heijden, M. G. A., J. N. Klironomos, M. Ursic, P. Moutoglis, R. Streitwolf-Engel, T. Boller, A. Wiemken, and I. R. Sanders. 1998b. Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 395: 69-72.
Wilson, G. W. T., and D. C. Hartnett. 1998. Interspecific variation in plant responses to mycorrhizal colonization in tallgrass prairie. American Journal of Botany 85: 1732-1738.

PART ONE:

Sampling Techniques Influence Understory Plant Trajectories Following Restoration-- An Example from Ponderosa Pine Restoration

ABSTRACT

While there is no one correct technique for sampling vegetation, the sampling design chosen may greatly influence the conclusions researchers can draw from restoration treatments. Considerations when designing vegetation sampling protocol include determining what sampling attributes to measure, the size and shape of the sampling plot, the number of replicates and their location within the study area, and the frequency of sampling. We installed 20 point-intercept transects (50-m long), 8 belt transects (10 x 50-m), 10 adapted Daubenmire transects (four 0.5 x 2-m plots) and 4 Modified-Whittaker plots (20 x 50 m with smaller nested plots) in treatment and control units to measure understory herbaceous response in a forest restoration experiment that tested different treatments. Point-intercept transects on average recorded at least twice as much plant cover as did adapted Daubenmire transects and Modified-Whittaker plots taken at the same location for all control and treatment units. Point-intercept transects and adapted Daubenmire plots on average captured fewer rare and exotic species in the control and treatment units in comparison to the belt transects and Modified-Whittaker plots. Modified-Whittaker plots captured the highest species richness in all units. Early successional understory response to restoration treatments was likely masked by the response of the herbaceous community to yearly climatic variation (dry vs. wet years). Species richness and abundance were higher in wet years than dry years for all control and treatment units. Our results illustrate that sampling techniques can greatly influence understory plant trajectories and therefore the interpretation of whether restoration goals have been achieved. In addition, our results suggest that restoration monitoring need to be conducted for a sufficient length of time so that restoration treatment responses can be detected.

INTRODUCTION

Ecological monitoring is a major component of numerous ecological restoration projects. Monitoring is the repetition of measurements over time for the purpose of quantifying change (MacDonald 1991), providing information about plant populations, community processes, and management techniques (Sutter 1996). Monitoring is often the tool used to define "success" in restoration projects and provides the justification for restoration treatments by being able to quantify restoration treatment effects (Sauer 1998). As a result, choosing an appropriate monitoring design that is compatible with the restoration project goals is crucial to the evaluation of any ecological restoration treatment.

Numerous vegetation sampling techniques are outlined in sampling textbooks (Mueller-Dombois and Ellenberg 1974; Krebs 1989; Kent and Coker 1994; and Barbour et al.1999) and in the scientific literature (Etchberger and Krausman 1997; Stohlgren et al. 1995a; Stohlgren et al. 1998) for quantifying different plant community attributes. Determining the sampling technique that is most appropriate for restoration monitoring

goals, however, can be difficult since there is no one "correct" sampling technique applicable to all study designs. First, restorationists need to determine what type of plant community attributes must to be measured in order to quantify restoration goals. Some frequently measured plant community attributes in restoration monitoring include species composition, richness, cover, density, frequency, and productivity. Second, restorationists need to make decisions about plot size and shape and the frequency and location of measurements (Stohlgren 1994). Finally, Sutter (1996) outlined four criteria of monitoring techniques that must be met in order to reliably and precisely detect change. These included: (1) data need to have a known and acceptable level of precision; (2) data sampling techniques need to be repeatable; (3) data need to be collected for a long enough time to capture responses to treatments; and (4) techniques need to be feasible, realistic, and inexpensive enough to be maintained long-term. In addition, monitoring techniques need to be adaptable so that new variables that were not anticipated at the beginning of the study can be incorporated into the existing monitoring protocol.

Currently, extensive efforts are underway to restore ponderosa pine forests across the western United States. Ponderosa pine restoration aims to reverse the degradation caused by historical land management practices of heavy grazing, intensive logging of old-growth trees, and fire suppression. Ponderosa pine forests are driven by a vital ecological attribute-fire. Prior to Euro-American settlement, low-intensity surface fires carried by the herbaceous understory were prevalent every 2-20 years in southwestern ponderosa pine forests and played a major role in regulating the structure, composition, and stability of these ecosystems (Fulé et al. 1997). A major goal of ponderosa pine restoration is restoring ecosystem structure and function within a range of natural variability. Two major components of ponderosa pine restoration are the reduction of high tree densities through tree thinning and the reintegration of the natural disturbance regime through prescribed burning.

Increasing species diversity and abundance of the native herbaceous understory is a major element to restoring ecosystem structure in southwest ponderosa pine systems (Covington et al. 1997). It is therefore important to have a monitoring sampling technique that will reliably and precisely detect change in the herbaceous understory of ponderosa pine forests where restoration treatments have been conducted. In particular, early detection of exotic and rare species in restoration treatment areas is fundamental to assessing the "success" of restoration projects because exotics can be problematic and because rare natives are often given special management attention. In addition, quantifying changes in overall herbaceous abundance is important in ponderosa pine restoration because a productive understory is necessary to carry natural or prescribed low-intensity fires that are integral to restoring these communities. As a result, we determined that species richness and species abundance were the two most important plant community attributes to monitor so that we could quantify if restoration goals for the herbaceous understory in southwestern ponderosa pine forests were achieved.

We were concerned that different monitoring sampling techniques that quantify species richness and abundance and different sampling sizes would result in inconsistent data and that these results would affect our ability to detect change in the herbaceous understory response to restoration treatments. The specific objectives of this study were to: 1) compare four sampling techniques with equal sample sizes to quantify changes in

herbaceous species richness and abundance in control and restoration treatment units; 2) compare four sampling techniques with unequal sample sizes in the same experimental setting; and 3) determine the effect of yearly climatic variation on the ability of different sampling techniques to detect change in response to restoration treatments.

METHODS

Experimental Design

We established three blocks of four different treatments during the summer of 1998 within an approximate 688 hectare area of the Fort Valley Experimental Forest and adjacent Coconino National Forest. Each treatment unit is approximately 16 hectares. Treatment units within each block were randomly assigned one of two treatments: (1) no thinning nor burning (control); and (2) thinning to a low level of trees more similar to the forest density prior to settlement, and prescribed burning at a later date.

The vegetation at the study site consists of pure ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stands, which contain a few large (>37.5 cm), yellow-barked ponderosa pine trees intermixed with numerous small black-barked ponderosa pine trees. Perennial grasses such as squirreltail (*Elymus elymoides*), mountain muhly (*Muhlenbergia montana*), Arizona fescue (*Festuca arizonica*), sedges (e.g., *Carex geophila)* and numerous forbs (*Antennaria* sp., *Cirsium* sp., *Lupinus argenteus, Solidago* sp.) dominate the understory. Soils are moderately well-drained clay and clay loams that are of volcanic origin (Covington et al. 1997). Annual precipitation ranges from 43 to 64 cm with an average of 50 cm in the Flagstaff area (Shubert 1974). Precipitation patterns follow scattered snowfall and rain during the winter months and a pronounced drought in May and June, followed by frequent monsoon rains in July and August (Vose and White 1991). Daily mean temperatures range from –5° C to 17° C (Sackett 1980).

Field Sampling

Four different vegetation monitoring techniques were established in the three control units and the three replicate treatment units. The original monitoring sampling design consisted of 20 systematically located permanent plots on a grid system within each unit. All vegetation sampling techniques were overlaid on this grid system. The four sampling techniques consisted of (1) the point-intercept method, (2) an adapted Daubenmire transect, (3) a belt transect, and (4) a Modified-Whittaker plot. We chose the first three sampling techniques because they are traditional sampling techniques that are well established and commonly used in monitoring vegetation. We chose the Modified-Whittaker plot design because recent studies have illustrated that it is more robust at capturing species diversity than traditional sampling techniques (Stohlgren et al. 1998). Four randomly located plots on the 20-plot grid system were chosen in each unit for a direct, paired comparison of the four techniques, hereafter referred to as the paired sampling technique comparisons. Figure 1 illustrates the layout of the sampling techniques at each plot. In addition, we compared the four techniques based on the total area sampled for each method; hereafter referred to as the unpaired sampling technique comparisons. For this comparison, the number of sampling plots in each unit was: 20 point-intercept transects, 10 Daubenmire transects, 8 belt transects, and 4 Modified-Whittaker plots. We used twenty point-intercept transects for each unit because this was the original sampling protocol for the study. We used 10 Daubenmire transects so that the average area recorded for plant foliar cover (40 m^2) was the same between this

technique and the 4 Modified-Whittaker plots within each unit. Finally, we used eight belt transects so that the average area recorded for species composition (4000 m^2) was the same between this technique and the 4 Modified-Whittaker plots within each unit. For both the paired and unpaired sampling techniques we recorded the amount of time it took to survey the vegetation, which did not include the time to set up the plots. We collected this information so that we could determine the cost of the different sampling techniques in comparison to the amount of data we collected (e.g., species richness).

General vegetation and site characteristic data were also collected to determine restoration treatment affects on other community attributes. Overstory tree data were collected in 400 m^2 circular plots centered on the plot center of each point-intercept transect. Tree species and diameter at breast height (dbh, 1.37 m) were recorded for all live and dead trees greater than 1.37 m in height. Tree canopy cover was determined by recording the presence or absence of tree canopy from a vertical projection at 30 cm intervals along the 50-m point-intercept transect. We used a 15-m planar transect located in a random direction from the plot center to measure forest floor litter and duff depths. Every 1.5 m, litter and duff were recorded following guidelines outlined in Brown (1974).

Point-intercept Transect

The point-intercept method uses a 50-m transect laid parallel to the environmental gradient (Figure 1). The primary objective of the point-intercept transect is to quantify plant foliar frequency, as a surrogate for plant cover/abundance (Buckner 1985). Every 30 cm along the transect, for a total of 166 point measurements, plant and substrate (litter, rock, wood, or bare mineral soil) was recorded using a point that varied between 5-10 mm. For all plant hits, the species was identified and its height was recorded. Plant abundance was determined by dividing the number of first plant hits by 166 points. Individual species abundance was determined by dividing the number of individual species' hits by the total number of plant hits.

Daubenmire Transect

One adapted Daubenmire transect, consisting of four 0.5 x 2 m plots, was overlaid on each line-intercept transect. Plots were located at 10, 20, 30, and 40 m alternating to the left and right of the transect (Figure 1). The main objective of the Daubenmire transect is to quantify plant foliar cover of most species in an area (Stohlgren et al. 1998). Daubenmire plant cover classes (e.g., 0-5, 5-25, 25-50%, etc.) were not used because they tend to overestimate species cover because the smallest size class averages cover to be 2.5 %/species. Instead, for each plot we estimated the percent cover of each species to the nearest quarter percent using cardboard cutouts of known sizes as visual guides. Ocular estimation of plant cover is a commonly used method for determining plant dominance, succession, and treatment response in vegetation analysis (Hatton et al. 1986). The estimates can total > 100% because percent cover was estimated independently for each species and independent of canopy position. Individual species abundance was determined by averaging the species' abundance in the four plots/transect. The percent cover of litter, rock, wood, and bare mineral soil was also determined for each plot.

Belt Transect

A 10 x 50 meter belt transect was centered over each 50-m line intercept transect (Figure 1). The primary objective of the belt transect is to obtain a species list of the area

(Kent and Coker 1994). All herbaceous and shrub species within the belt were recorded. We did not record any plant cover or substrate data.

Modified-Whittaker Plot

We placed the Modified-Whittaker plot (Stohlgren et al. 1995b) to the left of the line-intercept transect at 0 meters (Figure 3.1). The Modified-Whittaker plot is a 20 x 50-m nested plot design consisting of 10 1-m^2 plots with detailed plant and substrate information (six systematically arranged around the inside of the 1000-m^2 plot perimeter and four systematically arranged around the outside of the 100-m^2 perimeter), two 10-m^2 plots (in diagonally opposite corners of the plot), one 100-m^2 plot (in plot center), and one 1000-m^2 plot that documents species composition. The main objectives of the Modified-Whittaker plot are to quantify plant foliar cover and height for most species at an area, provide cover and frequency data that has low spatial autocorrelation, and to develop species-area curves based on the nested design to predict the number of species in a larger area (Stohlgren et al. 1995). Within each 0.5 x 2 m plot (1 m^2), species cover was estimated using the ocular estimate method to the nearest quarter percent similar to the methodology described for the adapted Daubenmire transects. Individual species abundance was determined by averaging the species' abundance of the ten 1-m^2 plots per a Modified-Whittaker plot. In addition, mean plant height and different substrate covers were also documented for each 1 m^2 plot.

Statistical Analyses

Multivariate analysis of variance (MANOVA) repeated measures was used to determine the effects of different sampling techniques and time on herbaceous species richness and abundance in control and treatment units for data collected in 1999 and 2000. We used the Shapiro Wilks test to determine if data met the normality assumption and Leven's test if data met the homogeneity of variance assumption (Milliken and Johnson 1984). Tukey's Honestly Significant Difference (HSD) test was used to make post-hoc multiple comparisons of means between sampling techniques. Significant differences were accepted at alpha ≤ 0.05. PC-ORD software was used to determine variation in community assemblages (herbaceous species richness and abundance combined) between different sampling techniques using non-metric multidimensional scaling (NMDS) and multi-response permutation procedures (MRPP) (McCune and Mefford 1999). Plant community data were relativized to the maximum prior to analysis to omit noise caused by very rare species and NMDS scree plots were determined to select the appropriate dimensionality in NMDS analysis.

RESULTS

Restoration thinning treatments influenced vegetation characteristics (Figure 2). There was a significant difference in trees/acre and tree canopy cover between pretreatment and post-treatment for the thinned units (Table 1). There was no significant difference between pretreatment and post-treatment trees/acre and tree canopy cover in the controls (no thinning/burning) (Table 1). In addition, there was no significant different difference between litter and duff loads between pretreatment and post-treatment in control or thinned units (Table 1).

Paired Sampling Technique Comparisons

The four different sampling techniques that were paired for a direct comparison within the control and treated units had greater variation in species richness than plant

foliar cover. The point-intercept transects recorded a significantly lower number of species for both years in the control and treatment units in comparison to the other three techniques (Figures 3a and 3b). The Modified-Whittaker plots recorded the highest number of species out of the four sampling techniques (Figures 3a and 3b). In addition, the Modified-Whittaker plots recorded a significantly higher number of exotic and annual species for both years than any of the other sampling techniques (Table 2). The point-intercept transects captured the fewest exotic and annual species, followed by the Daubenmire transects and belt transects; however, these differences were not significant. There was no significant difference between the number of species recorded in the treatment units between 1999 and 2000. Similarly, there was no significant difference between the number of species recorded in the control units between 1999 and 2000. However, species richness was lower in 2000 for all the control and treatment units than in 1999 (Figures 3a and 3b). Plant foliar cover was not significantly different in the control units between the three sampling techniques (Figure 4a). In contrast, in the treatment units, average foliar cover values were significantly higher in 1999 and 2000 using point-intercept transects than Daubenmire plots and Modified-Whittaker plots (Figure 4b).

Modified-Whittaker plots took significantly longer ($p=.001$) on average than the other sampling techniques to survey four replicates. Modified-Whittaker plots took an average of 341 minutes for one person to survey four plots in comparison to 55 minutes for four point-intercept transects, 43 minutes for four Daubenmire transects, and 46 minutes for four belt transects.

Unpaired Sampling Technique Comparisons

The four different sampling techniques had significant variation for species richness and plant foliar cover within control and treated units for both years with uneven replicates of sampling techniques in each unit: 20 point-intercept transects, 10 Daubenmire transects, 8 belt transects, and 4 Modified-Whittaker plots. Similar to the paired sampling technique comparisons, the point-intercept transects recorded the lowest number of species for both 1999 and 2000 in comparison to the other three techniques even with an additional 16 transects within each unit (Figures 5a and 5b). The belt transects recorded a significantly higher number of species than the previous two sampling techniques although it was not significantly different from the Modified-Whittaker plots (Figures 5a and 5b). Similar to the paired sampling technique comparisons, the line-intercept transects captured the fewest exotic and annual species, followed by the Daubenmire transects; however, these differences were not significant (Table 3). The belt transects and Modified-Whittaker plots recorded significantly more exotic and annual species than the other two sampling techniques (Table 3). For example, Dalmatian toadflax (*Linaria dalmatica* (L.) P. Mill.) was recorded in all three treatment units and one control using the belt transects and the Modified-Whittaker plots but was only recorded in one treatment unit using the line-intercept transects and Daubenmire transects. Similarly, Rusby's Milkvetch (*Astragulus rusbyi* Greene) was recorded in only one treatment or control unit using the line intercept transects and Daubenmire transects. In contrast, it was found in two controls and two treatment units using the Modified-Whittaker plot and in two control and one treatment unit using the belt transect. This species is listed as a threatened species by the state of Arizona. The Modified-Whittaker plots offer good detection of exotic and rare species and the ability

to quantify change in abundance where the belt transects only offer good detection because no cover values are recorded with belt transects.
There was no significant difference between the average number of species recorded in the control between 1999 and 2000 and treatment units between 1999 and 2000. However, there was lower species richness in 2000 than 1999 for all of the control and treatment units (Figures 5a and 5b). The point-intercept transects recorded significantly higher plant foliar cover than Daubenmire transects and Modified-Whittaker plots in both the control and treatment units in 1999 and 2000 (Figures 6a and 6b). Specifically, foliar cover from the point-intercept transects was more than double the average foliar cover from the Daubenmire transects and Modified-Whittaker plots.

Combining species composition data along with species abundance data allowed us to test whether community assemblages varied using different sampling techniques. Herbaceous community analysis using NMDS showed there were significant differences in community assemblages between the different sampling techniques that measured species richness and abundance (Figure 7).
There was no significant difference between the average time it took for one person to survey four Modified-Whittaker plots (341 minutes) in comparison to 20 point-intercept transects (321 minutes). Daubenmire transects and belt transects took significantly less ($p=.001$) time with an average of 128 minutes to survey 10 Daubenmire transects and an average of 133 minutes to survey 8 belt transects for one individual.

DISCUSSION

It is important that restoration practitioners and ecologists understand that designing monitoring protocol for restoration projects conducted strictly for restoring a system's ecological integrity (SER 1996) and designing monitoring protocol for ecological and restoration research are not always the same. A primary difference is that the majority of restoration projects are not duplicated across the landscape, which is often a prerequisite for any type of research design protocol. In addition, control areas (where restoration treatments have not taken place) are often not monitored in projects conducted strictly for restoration and not research. While inferences still can be made using traditional statistics to quantify differences from restoration treatments, these inferences are not as strong had they been repeated across the landscape and controls monitored. There are many similarities between restoration projects conducted strictly for restoring ecological integrity and those designed for both restoring ecological integrity and research. Some of these similarities include choosing the appropriate sampling attributes to answer the project's goals, identifying sampling techniques that have an acceptable level of precision, and addressing personnel and financial constraints--over 70% of all ecological studies are of three years or less due to funding constraints (Tilman 1989). Therefore, regardless whether restoration is being conducted solely for the purpose of restoring ecological integrity or for restoring ecological integrity and research, decisions must be made about determining appropriate sampling attributes and thus sampling techniques for quantifying restoration goals.

Species Richness

Species diversity is one of the most frequently sampled attributes in vegetation studies (Ricklefs and Schluter 1993) and increasing native plant diversity is one of the most cited goals of ecological restoration (e.g., Bugg et al. 1997, Johnson 1996,

Kindscher and Tieszen 1998). Species diversity is often used interchangeably with species richness. Species richness however is one of two components that define species diversity, the other being species evenness (Kent and Coker 1994). Having a sampling technique that is robust in capturing species richness should be desirable in restoration monitoring protocol unless increasing or decreasing plant abundance is the only goal of the project. The value of species richness data in restoration studies is not the actual number of species (e.g., 10 natives species would be more desirable than 30 non-native species) but rather species composition. Specifically, using species richness data to classify species into different groups based upon nativity, functional groups (e.g., nitrogen-fixers, photosynthetic pathways) and life-history traits is valuable in identifying whether restoration goals are met. Therefore, if understanding species composition is important to the goals of the restoration project than it is crucial to use a sampling technique that will detect less abundant (species with less than 1 percent cover) and rare species. Because restoration projects are often restricted by financial and time restraints, the sampling technique chosen must not only maximize the detection of species richness but also must be within financial and time restraints. In addition, determining the appropriate scale for capturing species diversity is important for restorationists because relationships between species richness and other community attributes such as productivity can be dependent upon the scale of study (Grytnes 2000). For example, a recent study by Stohlgren and others (1999) found that at the 1-m^2 plot scale areas rich in species were less invaded by exotic species; however, at the 1000-m^2 plot scale areas rich in species were the most heavily invaded by exotic species.

In our study the Modified-Whittaker plot served as the baseline for species richness comparisons because it captured the most species. Assuming there is some true number of species, the method that captures the highest species richness must be closest to the "truth." The direct comparison of sampling techniques at one location supported the well-known concept that an increase in sampling area will increase species richness detection (Rapson et al. 1997). The grain (the minimal scale sampled), the extent (the farthest distance between samples), and the number of samples influence the positive relationship between species richness and area (Palmer and White 1994). In our study, the point-intercept transect sampled the smallest total area (< 0.1-m^2) and found the fewest species, followed by the Daubenmire transect (4-m^2), the belt transect (500-m^2) and the Modified-Whittaker plot (1000-m^2), which captured the most species. When more belt transects were added so that the sampling area was equal to the area surveyed in Modified-Whittaker plots there was no significant difference in species richness, although Modified-Whittaker plots returned slightly higher numbers.

Other methodology comparison studies in various ecosystems have documented low species detection using point-intercept transects in comparison to other sampling techniques (Kinsinger et al. 1960, Etchberger and Kraussman 1997, Stohlgren et al. 1998). A high degree of spatial autocorrelation is another possible reason, in addition to their small sampling area, why transect methods failed to capture higher levels of species richness (Stohlgren et al. 1998). Due to the spatial arrangement of the sampling technique, point-intercept transects and Daubenmire transects tend to record redundant information on species richness while at the same time missing many species (Stohlgren et al. 1998). However, in our study Daubenmire transects captured significantly more

species than the point-intercept transects, which is probably the result of the larger sampling area surveyed.

Modified-Whittaker plots on average took five times longer for one individual to survey four plots in comparison to sampling four replicates of the other sampling techniques. Modified-Whittaker plots also captured five times as many species as the point-intercept technique for the paired sampling technique comparisons. There was no significant difference between the time it took one individual to survey four point-intercept transects, four Daubenmire transects and four belt transects. However, Daubenmire transects captured twice as many species, and belt transects captured three times as many species, as the point-intercept transects. For the unpaired sampling technique comparisons there was no significant difference between the time it took one individual to survey four Modified-Whittaker plots in comparison to 20 point-intercept transects, although on average the four Modified-Whittaker plots captured over twice as many species as the 20 point-intercept transects. In addition, there was no significant difference between the amount of time it took to survey ten Daubenmire transects and eight belt transects but belt transects captured twice as many species. Finally, there was no difference between the average number of species captured using eight belt transects in comparison to four Modified-Whittaker plots even though the eight belt transects took less than half the time to survey. These data illustrate how the amount of data collected is related to the time it takes to collect the data.

The type of sampling technique chosen to measure herbaceous species richness in restoration studies needs to incorporate the amount of time available for sampling, the detail of information required, and the focus of the herbaceous understory in a multi-objective sampling design that incorporates other landscape parameters such as fuels, trees, etc. For example, if only a species list is needed, the belt transect provides the most information for the cost. Alternatively, if a species list, species abundance data, and capturing rare and exotic species is important then the Modified-Whittaker plot provides the most information for the cost. As a result, restoration ecologists need to clearly identify restoration goals before the most appropriate sampling method for measuring plant community attributes can be determined.

Species Abundance

Increasing native herbaceous foliar cover is an important goal in many ecological restoration treatments (Covington et al. 1997, Lovich and Bainbridge 1999) and therefore it is important to have a robust sampling technique to accurately measure foliar cover included in restoration monitoring. Species abundance is some measure of the amount of a species in a sample (Chiarucci et al. 1999). Plant community attributes that measure species abundance include plant foliar cover, plant density, and plant frequency. Plant foliar cover is one of the most widely used abundance measurements because it is not biased by the size or distribution of individual species as plant density and plant frequency measurements can be (Floyd and Anderson 1987). Ecologists have designed numerous sampling techniques to quantify plant foliar cover. The three most commonly used techniques include the point-intercept, the line-intercept, and ocular estimation (Buckner 1985), all of which have been used in restoration studies. These three methods all have strengths and weaknesses, but when used appropriately their weaknesses can be minimized. Therefore, restorationists need to weigh the benefits of the different

techniques and their compatibility with overall restoration project goals (e.g., financial and time limitations).

Point-Intercept

It is difficult to determine a baseline for foliar cover as was done with species richness because the sampling techniques in our study produced varied results and the actual cover of individual species in the treatment units is unknown. Because one technique provides more species cover than another technique does not necessarily mean that the technique providing the higher cover is more accurate. Regardless, we can draw some general conclusions about the two sampling techniques used in this study from other published data that have compared these sampling techniques and their precision. The point-intercept transect is a very robust technique for measuring foliar cover when it is used appropriately (Brady et al. 1995). This sampling technique was designed to be limited to a "dimensionless" point where the probability of a particular species being contacted by a point is a strict function of its abundance (Buckner 1985). This requirement is often violated because of the extra time needed to sample small points with a vertical projection, thereby compromising the accuracy and objectivity of the method. Researchers have shown, however, that the violation of point size and point projection can be minimized when an optical device with fine cross hairs is attached to a sturdy tripod.

In our study, the point-intercept method recorded twice as much foliar cover as the Daubenmire transects and Modified-Whittaker plots in the paired sampling technique comparisons. Point-intercept plant foliar cover values were almost three times higher than Daubenmire transect and Modified-Whittaker plot values in the unpaired sampling technique comparisons. These results are consistent with other studies that have documented an overestimation of foliar cover when point-line intercept transects were not used appropriately (Sharp 1954, Buckner 1985, Frank and McNaughton 1990, Stohlgren et al. 1998). As early as 1952, Goodall illustrated the large effect that point size has on cover values. For example, when measuring cover of a grass species he found that a pin diameter of 4.75 mm recorded a cover of 71 percent, a pin diameter of 1.84 mm recorded 66.5 percent cover and pin diameter reduced to a point with almost no diameter resulted in 39 percent cover. Similarly, Wilson (1963) found that the error in cover estimates doubled with a doubling of the pin diameter or halving of the leaf breadth. In addition, he found that there was an interaction between pin diameter and leaf size, preventing the use of an error correction value because leaf size will vary with age and environment (Wilson 1963).

Our original sampling technique was designed to be consistent with the prescribed fire monitoring protocol currently being used across the western United States to measure herbaceous response to prescribed fire. In our study, we used a point that varied between 5-10 mm and a point that was not controlled for vertical projection. These two violations of the point-intercept sampling technique, along with the comparison of our data with other studies that used a similar point size, suggests that our point-intercept foliar cover values overestimated the actual foliar cover. Other evidence that suggests our sampling technique overestimated cover includes a study that found systematically located points overestimated foliar cover in comparison to randomly located points along a transect (Whysong and Miller 1987) and a study that found species with small, outstretched leaves such as grasses and legumes increased pin contact and therefore overestimated

their cover (Glatzle et al. 1993). In our study we used systematically located points along a transect to measure cover and our vegetation was dominated by grasses and sedges.

Ocular Estimation

Visual estimation of plant cover is one of the most common measurements in plant ecology and restoration studies (Kennedy and Addison 1987). Ocular estimates are normally taken within a 1 m^{-2} area because one of the requirements for accuracy is that observations must be made from a vertical perspective within a bounded plot (Buckner 1985). Ocular estimates can either be estimated to the nearest predetermined percent (e.g., closest 1 percent) or they can be categorized into published cover classes (e.g., Daubenmire or Braun-Blanquet, Mueller-Dombois and Ellenberg 1974). In this study we did not categorize ocular estimates into published cover classes because of the inherent problems with overestimating cover values when ocular estimates are categorized, which has been documented in numerous studies in many ecosystems (Floyd and Anderson 1987, Hatton et al. 1986, Stohlgren et al. 1998). Instead, we estimated cover values to the nearest quarter percent within 1-m^2 plots and used cutout visual aids of different percents as suggested by Tilman (1997) to reduce inconsistencies between observers. Even taking these measures to reduce bias in cover estimates, the mental integrations involved in ocular estimation make cover estimates inherently variable between observers, though observers experienced with the technique can be consistent within their own observations (Buckner 1985). A study by Sykes and other (1983) showed that there was reasonable agreement among observers using ocular estimation for 4-m^2 quadrats but that larger 50-m^2 and 200-m^2 quadrats had large inconsistencies between observer estimates with clear tendencies of some observers to consistently over- or underestimate cover. To increase consistency in ocular estimates it has been recommended that observers practice reading cover for species before sampling begins and to periodically compare values among observers throughout the field season (Anderson and Kothmann 1982). In our study, both the Daubenmire transects and the Modified-Whittaker plots used ocular estimates for species cover values. In the direct comparison plots (sixteen 1-m^2 plots for the Daubenmire transects and forty 1-m^2 plots in the Modified-Whittaker plots per a unit) there was no significant difference between foliar cover values using these two techniques in comparison with the point-intercept technique. In addition, there was no significant difference in foliar cover values between the two sampling techniques when both the Daubenmire transects and Modified-Whittaker plots had forty 1-m^2 plots within each sampling unit. This consistency between the two sampling techniques, along with the known violations made using the point-intercept technique, suggest that foliar cover values using ocular estimation were more accurate than foliar cover values using the point-intercept method.

CONCLUSION AND RECOMMENDATIONS

The sampling technique chosen for monitoring herbaceous species composition, richness, and foliar cover in restoration studies can greatly influence understory plant trajectories following restoration treatments. Reference conditions are often cited as the goal for restoration treatments. This study illustrates that the type of sampling technique used to determine reference conditions should be similar to the sampling technique used to monitor change or the data may lead to inaccuracy, confusion, or apparent over- or under-achievement of goals. Large area sampling techniques were the most effective at

capturing overall species composition and rare and exotic species. Modified-Whittaker plots returned on average the highest species richness in all sampling technique comparisons and captured the most rare and exotic species. In comparison, point-intercept transects captured the fewest species. Point-intercept transects using an optical device to eliminate error are recommended in revegetation studies where objectivity and repeatability are of primary importance and capturing species diversity is of secondary importance (Buckner 1985). In studies where capturing species diversity and cover values of rare and exotic species are of primary importance we recommend Modified-Whittaker plots. Determining the sampling technique that should be used for a particular study needs to take into consideration numerous factors such as the restoration goals, sampling attributes, level of sampling precision, and financial and personnel constraints. Also, when choosing a sampling technique for long-term monitoring of restoration treatments, it is important to test sampling techniques for specific sampling attributes to make sure they will meet the objectives of the particular study rather than simply using a particular sampling technique because it is well established and recommended.

Our study with two years post treatment data was not conducted over a long enough timeframe to detect foliar cover change in response to restoration treatments. Change in foliar cover was likely masked by the herbaceous community response to yearly climatic variation (dry vs. wet years). The year of 1999 was a wet summer (May-September) with 27.51 cm of rain in comparison to the summer of 2000, which received 11.26 cm of rain (NOAA). The average summer precipitation is 20.83 cm (NOAA). These changes in precipitation were evident in the herbaceous community with lower species richness and foliar cover in 2000 for the control and treatment units than recorded in 1999 for all units. The monitoring of the herbaceous understory in this study is part of a long-term restoration research project and will be sampled every year until 2003 and then every five years thereafter. We recommend that restoration monitoring be conducted for a length of time that is congruent with the ability to assess restoration goals adequately. If restoration monitoring does not extend through this timeframe, because of lack of funding to monitor, then the project will often be critiqued as being unsuccessful even if it may be successful with proper monitoring. We recommend that at a minimum permanent photo points are included in all restoration projects and that they be continued until restoration goals can be quantified. Therefore, it is necessary in the project's restoration goals to state how long it will take for these goals to be achieved and monitoring should be conducted at a minimum for this length of time and maybe longer if other variables such as yearly climatic variation are not taken into consideration in the original project goals. It is important as restoration ecologists that we learn from projects that are both critiqued as successful and unsuccessful, as defined by our restoration goals, and that we share this information with other restoration ecologists and practitioners so that the field of restoration ecology can be advanced.

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LITERATURE CITED

Anderson, D. M. and M. M. Kothmann 1982. A two-step sampling technique for estimating standing crop of herbaceous vegetation. Journal of Range Management 35(5): 675-677.

Barbour, M. G., Burk, J. H. and W. D. Pitts 1999. Terrestrial plant ecology. Third edition. Benjamin/Cummings Publishing Company, Menlo Park, California.

Brady, W. W. Mitchell, J. E., Bonham, C. D., and J. W. Cook 1995. Assessing the power of the point-line transect to monitor changes in plant basal cover. Journal of Range Management 48: 187-190.

Brown, J.K. 1974. Handbook for inventorying downed woody material. United States Department of Agriculture Forest Service General Technical Report INT-16, Intermountain Forest and Range Experiment Station, Ogden, UT.

Buckner, D. L. 1985. Point-intercept sampling in revegetation studies: maximizing objectivity and repeatability. American Society for Surface Mining and Reclamation, Denver, Colorado.

Bugg, R. L., Brown, C. S. and J. H. Anderson 1997. Restoring native perennial grasses to rural roadsides in the Sacramento Valley of California: establishment and evaluation. Restoration Ecology 5(3): 214-228.

Chiarucci, A., Wilson, J. B., Anderson, B. J., and V. De Dominicis 1999. Cover versus biomass as an estimate of species abundance: does it make a difference to the conclusions? Journal of Vegetation Science 10: 35-42.

Covington W. W., FulJ P. Z., Moore M. M., Hart S. C., Kolb T. E., Mast J. N., Sackett S. S., Wagner, M. R. 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. Journal of Forestry 95(4): 23-29.

Etchberger R. C., and P. R. Krausman 1997. Evaluation of five methods for measuring desert vegetation. Wildlife Society Bulletin 25(3): 604-609.

Floyd, D. A. and J. E. Anderson 1987. A comparison of three methods for estimating plant cover. Journal of Ecology 75: 221-228.

Frank, D. A. and S. J. McNaughton 1990. Aboveground biomass estimation with the canopy intercept method: a plant growth form caveat. Oikos 57: 57-60.

Fulé, P. Z., Covington, W. W., and M. M. Moore 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. Ecological Applications 7(3): 895-908.

Glatzle, A., Mechel, A. and M. E. Vaz Lourenco 1993. Botanical components of annual Mediterranean grassland as determined by point-intercept and clipping methods. Journal of Range Management 46: 271-274.

Goodall, D. W. 1952. Some considerations in the use of point quadrats for the analysis of vegetation. Australian Journal of Science Research, Series B 5: 1-41.

Grytnes, J. A. 2000. Fine-scale vascular plant species richness in different alpine

vegetation types: relationships with biomass and cover. Journal of Vegetation Science 11: 87-92.
Hatton T. J., West N. E. and P. S. Johnson 1986. Relationships of the error associated with ocular estimation and actual total cover. Journal of Range Management 39(1): 91-92.
Hinds, W. T. 1984. Towards monitoring of long-term trends in terrestrial ecosystems. Environmental Conservation 11(1): 11-18.
Johnson, B. R. 1996. Southern Appalachian rare plant reintroductions on granite outcrops in: Restoring diversity—strategies for reintroduction of endangered plants (eds D. A. Falk, C. I. Millar, and M. Olwell), Island Press, Washington, D.C.: 433-444.
Kennedy, K. A. and P. A. Addison 1987. Some considerations for the use of visual estimates of plant cover in biomonitoring. Journal of Ecology 75: 151-157.
Kent, M. and P. Coker 1994. Vegetation description and analysis: a practical approach. Chinchester, Wiley, New York.
Kindscher, K. and L. L. Tieszen 1998. Floristic and soil organic matter changes after five and thirty-five years of native tallgrass prairie restoration. Restoration Ecology 6(2): 181-196.
Kinsinger, F. E., Eckert, R. E. and P. O. Currie 1960. A comparison of the line-interception, variable-plot and loop methods as used to measure shrub-crown cover. Journal of Range Management 13: 17-21.
Krebs, C. J. 1989. Ecological methodology. Harper and Row, New York.
Lovich, J. E. and D. Bainbridge 1999. Anthropogenic degradation of the southern California desert ecosystem and prospects for natural recovery and restoration. Environmental Management 24(3): 309-326.
MacDonald, L. H. 1991. Monitoring guidelines to evaluate effects of forestry activities on streams in the Pacific Northwest and Alaska. Document EPA 910/9-91-001. Seattle, Washington: EPA.
Milliken, G. A. and D. E. Johnson 1984. Analysis of messy data, Vol. I. Designed experiments. Van Nostrand Reinhold Co., New York.
Mueller-Dombois, D. and H. Ellenberg 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.
Palmer, M. W. and P. S. White 1994. Scale dependence and the species-area relationship. The American Naturalist 144(5): 717-740.
Rapson, G. L., Thompson, K. and J. G. Hodgson 1997. The humped relationship between species richness and biomass-testing its sensitivity to sample qaudrat size. Journal of Ecology 85: 99-100.
Ricklefs R. E. and D. Schluter (eds.) 1993. Species diversity in ecological communities-historical and geographical perspectives. The University of Chicago Press, Chicago, Illinois.
Sackett S. S. 1980. Reducing natural ponderosa pine fuels using prescribed fire: Two case studies. USDA Forest Service Research Paper RM-392.
Sauer, L.J. 1998. The once and future forest. Island Press, Washington, D.C.
Sharp, L. A. 1954. Evaluation of the loop procedure of the 3-step method in the salt-desert shrub type in southern Idaho. Journal of Range Management 7:

83-88.
Shubert G. H. 1974. Silviculture of southwestern ponderosa pine: the status of our knowledge. USDA Forest Service Research Paper RM-123.
Stohlgren, T. J. Binkley, D., Veblen, T. T. and W. L. Baker 1995a. Attributes of reliable long-term landscape-scale studies: malpractice insurance for landscape ecologists. Environmental Monitoring and Assessment 36: 1-25.
Stohlgren, T. J., Falkner, M. B., and L. D. Schell 1995b. A Modified-Whittaker nested vegetation sampling method. Vegetatio 117: 113-121.
Stohlgren, T. J., Bull, K. A., and Y. Otsuki.1998. Comparison of rangeland vegetation sampling techniques in the Central Grasslands. Journal of Range Management 51: 164-172.
Stohlgren, T. J., Binkley, D., Chong, G. W., Kalkhan M. A., Schell L. D., Bull, K. A., Otsuki, Y., Newman, G., Bashkin, M. and Y. Son 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69: 25-46.
Sutter, R. D. 1996. Monitoring, in: Restoring diversity—strategies for reintroduction of endangered plants (eds D. A. Falk, C. I. Millar, and M. Olwell), Island Press, Washington, D.C.: 235-264.
Sykes, J. M., Horrill, A. D. and M. D. Mountford 1983. Use of visual cover assessments as quantitative estimators of some British woodland taxa. Journal of Ecology 71: 437-450.
Tilman, D. 1989. Ecological experimentation: strengths and conceptual problems. In: *Long-term Studies in Ecology*. Likens, G. E. (ed.) New York: Springer-Verlag,136-157.
Tilman D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78(1): 81-92.
Vose J. M. and A. S. White 1991. Biomass response mechanisms of understory species the first year after prescribed burning in an Arizona ponderosa-pine community. Forest Ecology and Management 40: 175-187.
Whysong, G. L. and W. H. Miller 1987. An evaluation of random and systematic plot placement for estimating frequency. Journal of Range Management 40(5): 475-479.
Wilson, J. W. 1963. Errors resulting from thickness of point quadrats. Australian Journal of Botany 11: 178-188.

Table 1 Vegetation and site characteristics for control and thinned units for pretreatment 1998 data and post treatment 2000 data. Data are expressed as means (N=3) ± SE.

	Pretreatment 1998		Post treatment 2000	
Variable	**Control Stand**	**Treatment Stand**	**Control Stand**	**Treatment Stand**
trees/hectare	1187.5 ± 307	1043.3 ± 442.6	1181.9 ± 302.5 a	242.89 ± 31.9 b
tree canopy cover (%)	64.9 ± 5.4	58.98 ± 5.3	61.8 ± 4.6 a	40 ± 2.9 b
litter load (kg/ha)	14211.5 ± 1508.04	14133.76 ± 1980.12	14363.7 ± 1508.04	15625.13 ± 2598.97
duff load (kg/ha)	25127.12 ± 2006.04	25338.22 ± 3266.01	25836.25 ± 3103.27	26379.49 ± 3266.01

Values indexed by a different letter are significantly different at the $p \leq 0.05$ level between paired control and treatment units for the same sampling year.

Table 2 Total number of exotic and annual species captured in 1999 and 2000 for paired plots using different sampling techniques in the control and treatment units with similar sampling sizes. Data are expressed as means (N=3) ± SE.

	Line-Intercept Transect	Daubenmire Transect	Belt Transect	Modified Whittaker Plot
Control Plots				
Exotic 1999	0 ± 0 a	0.33 ± .33 a	1.33 ± .33 b	2.33 ± .68 b
Exotic 2000	0 ± 0 a	0.33 ± .33 a	0.33 ± .33 a	2.00 ± .57 b
Annual 1999	0.66 ± .33 a	1.67 ± .33 a	2.33 ± .33 a	6.00 ± 1.52 b
Annual 2000	0 ± 0 a	1.00 ± .58 a	1.00 ± 0 a	3.33 ± .33 b
Treatment Plots				
Exotic 1999	0.33 ± .33 a	2.33 ± 1.33 b	3.00 ± 1.52 b	4.00 ± .64 b
Exotic 2000	0.67 ± .33 a	1.33 ± .88 a	3.00 ± 1.1 a	4.00 ± .57 b
Annual 1999	0.67 ± .33 a	3.67 ± 1.67 a	6.00 ± 1.5 a	10.00 ± 2.1 b
Annual 2000	0.67 ± .33 a	2.33 ± .88 a	5.67 ± 1.4 a	8.00 ± .58 b

Number of samples within a plot: line-intercept transect N=4, Daubenmire transect N=4, belt transect N=4, modified Whittaker plot N=4. Values indexed by different letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between different sampling techniques.

Table 3 Total number of exotic and annual species captured in 1999 and 2000 in the control and treatment units using different sampling techniques with different sampling sizes. Data are expressed as means (N=3) ± SE.

	Line-Intercept Transect	Daubenmire Transect	Belt Transect	Modified Whittaker Plot
Control Plots				
Exotic 1999	0 ± 0 a	0.33 ± .33 a	2.67 ± .33 b	2.33 ± .88 b
Exotic 2000	0.33 ± .33 a	0.33 ± .33 a	1.27 ± .33 b	2.00 ± .57 b
Annual 1999	2.67 ± .88 a	1.67 ± .33 a	5.33 ± .88 b	6.00 ± 1.52 b
Annual 2000	1.00 ± .58 a	1.00 ± .58 a	3.00 ± 1.33 b	3.33 ± .33 b
Treatment Plots				
Exotic 1999	0.67 ± .33 a	1.33 ± .88 a	3.67 ± .76 b	4.00 ± .64 b
Exotic 2000	1.00 ± .58 a	0.67 ± .67 a	3.67 ± .67 b	4.00 ± .57 b
Annual 1999	2.33 ± .67 a	3.67 ± .33 a	8.00 ± 3.0 b	10.00 ± 2.0 b
Annual 2000	2.67 ± .88 a	3.33 ± .33 a	7.00 ± 1.1 b	8.00 ± .58 b

Number of samples within a plot: line-intercept transect N=20, Daubenmire transect N=10, belt transect N=8, modified Whittaker plot N=4. Values indexed by different letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between different sampling techniques.

Figure Headings

Figure 1. Layout of the four sampling techniques for direct paired comparisons. The point-intercept transect is shown in hatch marks (50-m), the belt transect is outlined in dots (10 x 50-m), the adapted Daubenmire transect has four shaded plots (0.5 x 2-m) and the Modified Whittaker plot is shown in solid lines (20 x 50-m) with smaller nested plots of various sizes (ten 0.5 x 2-m plots, two 2 x 5-m plots and one 5 x 20-m plot).

Figure 2. Examples of the tree density, fuel loads, and understory vegetation in a thinned treatment unit (photo on left) and an uncut/unburned control unit (photo on right).

Figure 3a-b. Total species richness for paired control (a) and treatment (b) plots in 1999 and 2000 using four different sampling techniques. Data are expressed as means (N=4) ± SE. Values indexed by different letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between different sampling techniques. There was no significant difference between the number of species recorded between 1999 and 2000 for individual sampling techniques.

Figure 4a-b. Total plant foliar cover for paired control (a) and treatment (b) plots in 1999 and 2000 using four different sampling techniques. Data are expressed as means (N=4) ± SE. Values indexed by different letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between different sampling techniques. There was no significant difference between total plant foliar cover between 1999 and 2000 for individual sampling techniques.

Figure 5a-b. Total species richness for all control (a) and treatment (b) plots in 1999 and 2000 using four different sampling techniques. Data are expressed as means (N=20 point-intercept transect; N=4 adapted Daubenmire transects; N=8 belt transects; N=4 Modified-Whittaker plots) ± SE. Values indexed by different letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between different sampling techniques. There was no significant difference between the number of species recorded between 1999 and 2000 for individual sampling techniques..

Figure 6a-b. Total plant foliar cover for all control (a) and treatment (b) plots in 1999 and 2000 using four different sampling techniques. Data are expressed as means (N=20 point-intercept transect; N=4 adapted Daubenmire transects; N=8 belt transects; N=4 Modified-Whittaker plots) ± SE. Values indexed by different letters are significantly different at the $p \leq 0.05$ level as determined by Tukey's HSD test between different sampling techniques. There was no significant difference between total plant foliar cover between 1999 and 2000 for individual sampling techniques.

Figure 7. Ordination of plant community data for post-treatment 1999 and 2000 data determined with non-metric multidimensional scaling (NMDS) for three different sampling techniques: point-intercept transcects, Daubenmire plots, and Modified-Whittaker plots. Belt transect data were not included because species abundance values were not collected for this method. Each symbol represents the plant community for a specific unit and sampling technique. Plant communities that are more similar are found

closer together and plant communities that are more dissimilar are further apart. Plant community data were relativized to the maximum prior to analysis to omit noise caused by very rare species and NMDS scree plots were determined to select the appropriate dimensionality in NMDS analysis.

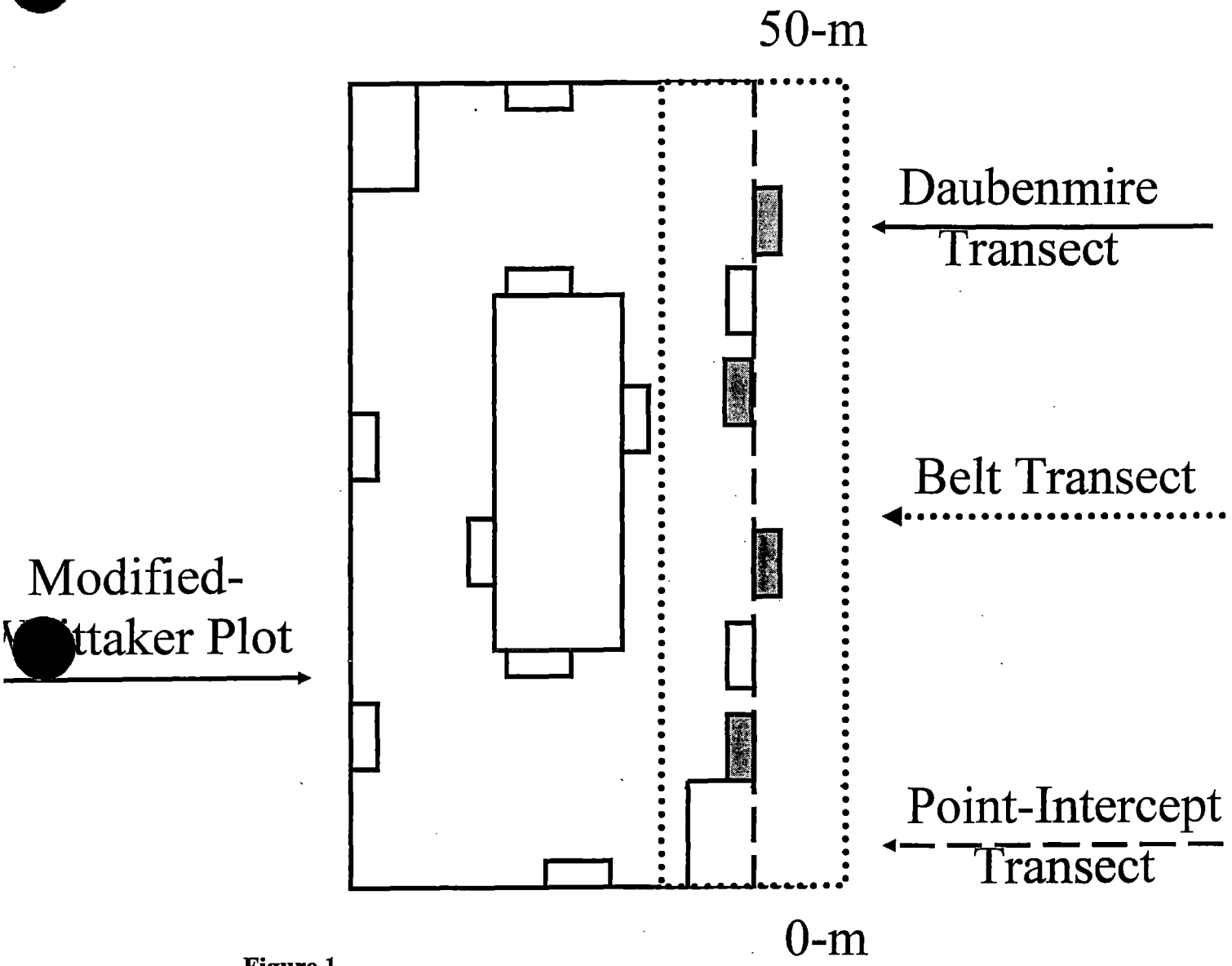
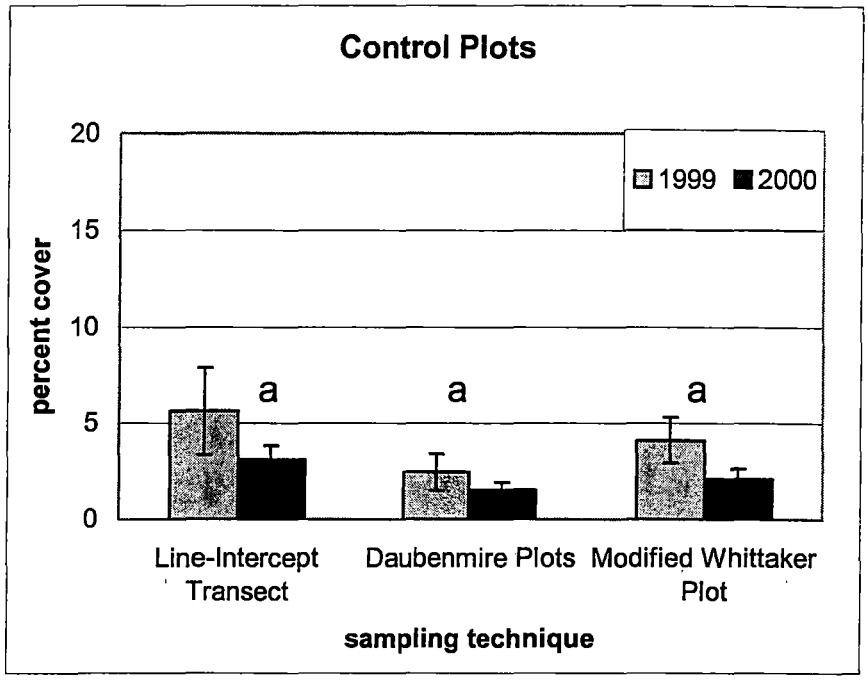

50-m
Daubenmire
Transect
Belt Transect
Modified-
ttaker Plot
Point-Intercept
Transect
0-m

Figure 1.

Figure 2.


Control Plots
20
15
10
5
0
percent cover
1999
2000
a
a
a
Line-Intercept Transect
Daubenmire Plots
Modified Whittaker Plot
sampling technique

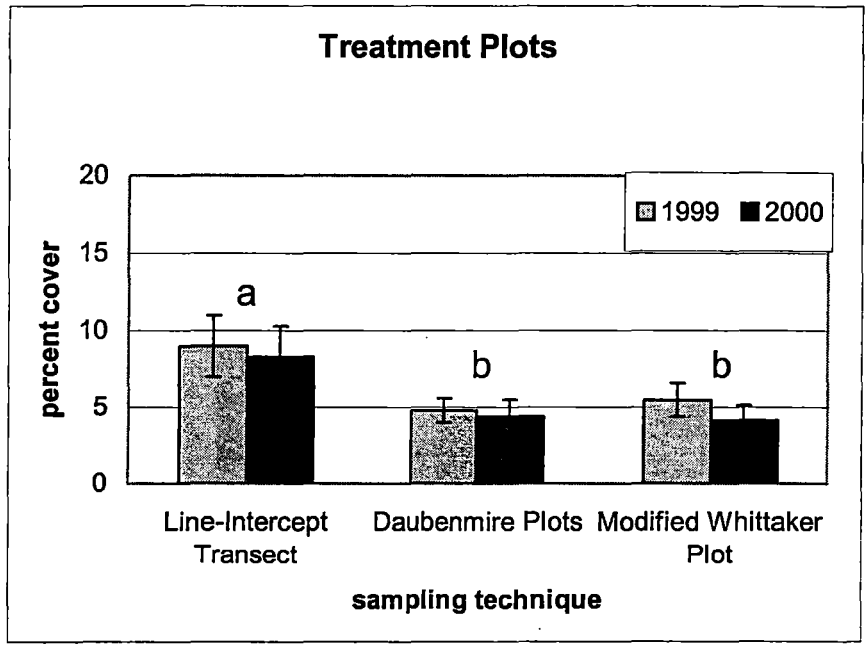
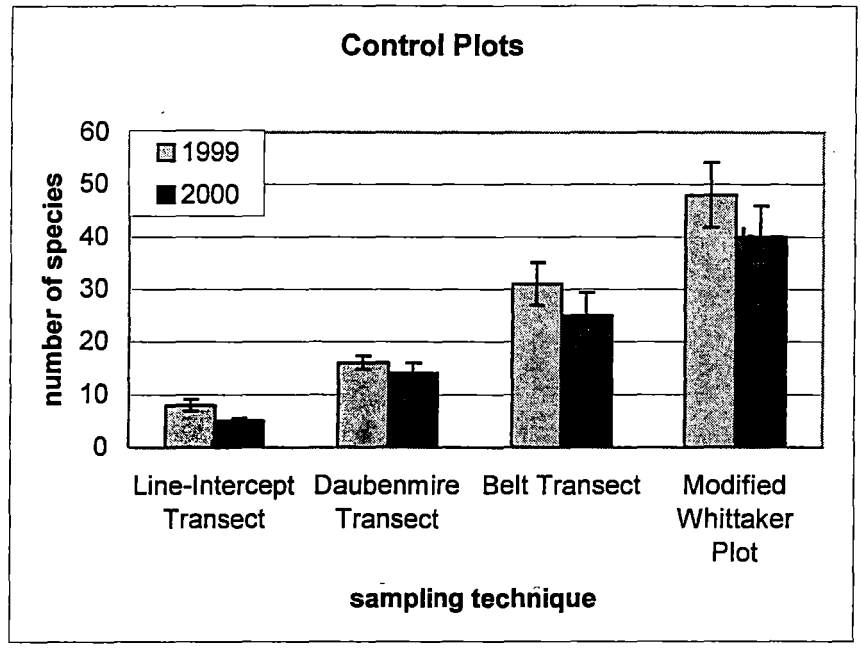

Treatment Plots
20
15
10
5
0
percent cover
1999
2000
a
b
b
Line-Intercept Transect
Daubenmire Plots
Modified Whittaker Plot
sampling technique

Figure 4a-b


Control Plots
60
50
40
30
20
10
0
number of species
1999
2000
Line-Intercept Transect
Daubenmire Transect
Belt Transect
Modified Whittaker Plot
sampling technique

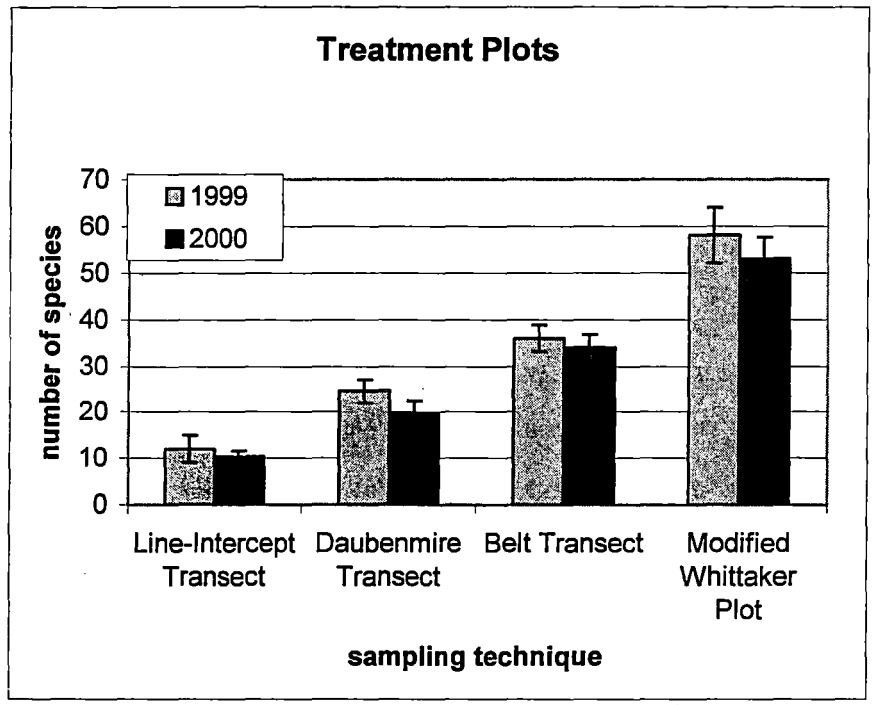
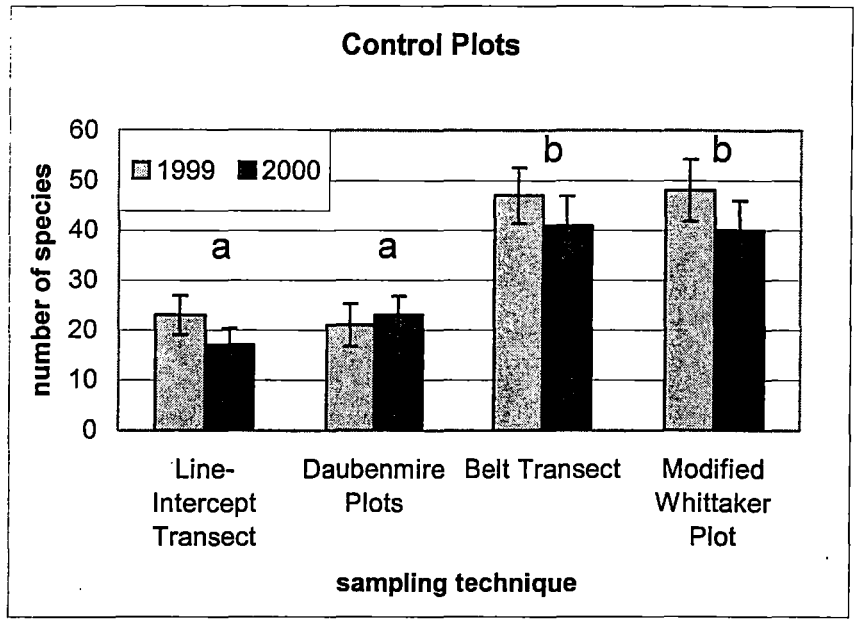

Treatment Plots
70
60
50
40
30
20
10
0
number of species
1999
2000
Line-Intercept Transect
Daubenmire Transect
Belt Transect
Modified Whittaker Plot
sampling technique

Figure 3a-b


Control Plots
number of species
60
50
40
30
20
10
0
1999
2000
a
a
b
b
Line-Intercept Transect
Daubenmire Plots
Belt Transect
Modified Whittaker Plot
sampling technique

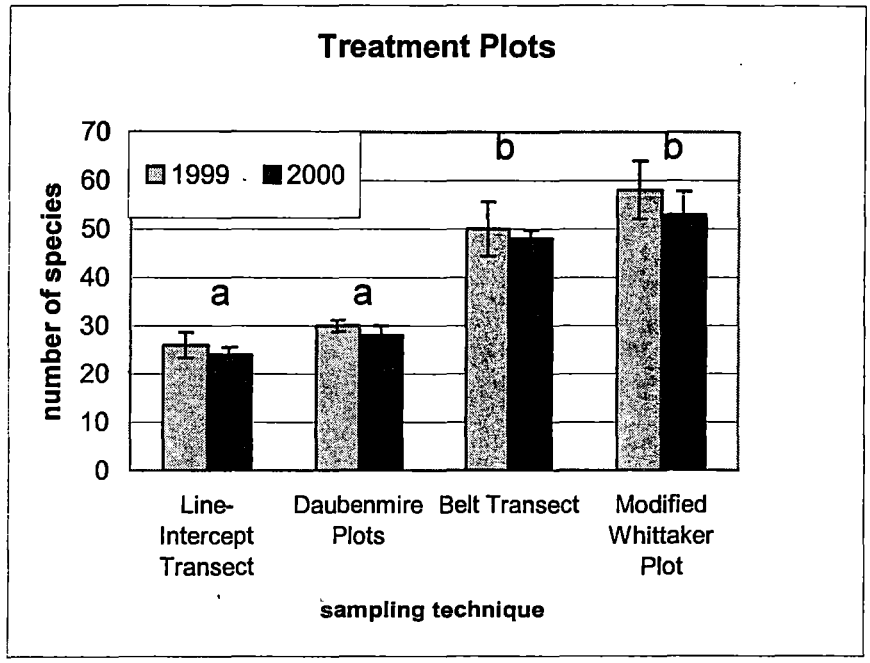
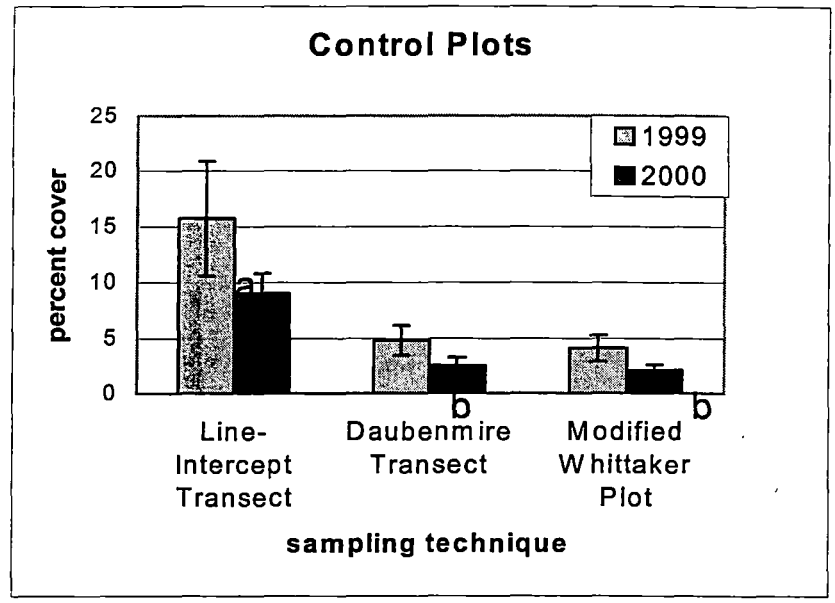

Treatment Plots
number of species
70
60
50
40
30
20
10
0
1999
2000
a
a
b
b
Line-Intercept Transect
Daubenmire Plots
Belt Transect
Modified Whittaker Plot
sampling technique

Figure 5a-b


Control Plots
25
20
15
10
5
0
percent cover
1999
2000
a
b
b
Line-Intercept Transect
Daubenmire Transect
Modified Whittaker Plot
sampling technique

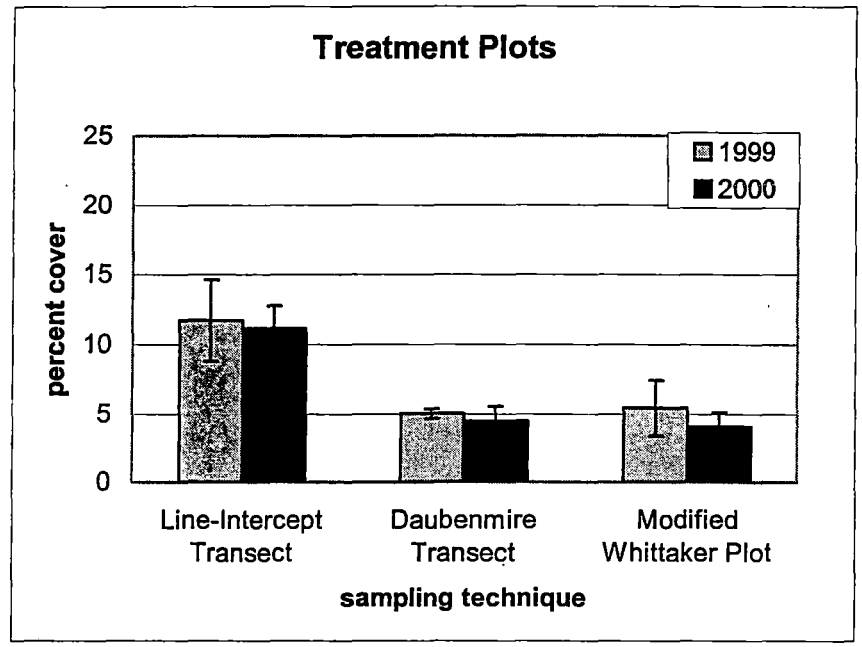

Treatment Plots
25
20
15
10
5
0
percent cover
1999
2000
Line-Intercept Transect
Daubenmire Transect
Modified Whittaker Plot
sampling technique

Figure 6a-b

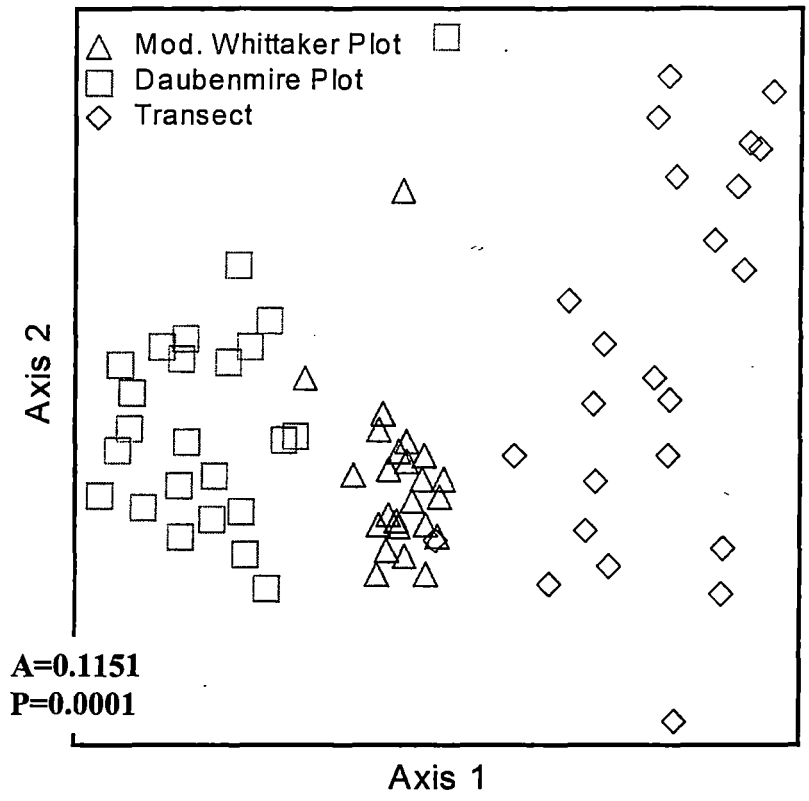

Mod. Whittaker Plot
Daubenmire Plot
Transect
Axis 2
A=0.1151
P=0.0001
Axis 1

Figure 7.

Arbuscular mycorrhizal propagule densities respond rapidly to ponderosa pine restoration treatments

SUMMARY

1. Mycorrhizae form a critical link between aboveground plants and the soil system by influencing plant nutrition, nutrient cycling, and soil structure. Understanding how mycorrhizae respond to disturbances may lead to important advances in interpreting aboveground plant recovery.

2. The inoculum potential for arbuscular mycorrhizae (AM) and ectomycorrhizal (EM) fungi was investigated in thinned only, thinned and prescribed burned (both restoration treatments) and unthinned and unburned control stands in northern Arizona ponderosa pine forests. The relationships between mycorrhizal fungal propagule densities and plant community and soil properties were quantified.

3. The relative amount of infective propagules of AM fungi was significantly higher in samples collected from both restoration treatments than their paired controls (unthinned and unburned stands). In contrast, the same restoration treatments had no significant effect on the relative amount of infective propagules of EM fungi.

4. The relative amount of infective propagules of AM fungi was significantly positively correlated with graminoid cover and herbaceous understorey species richness and negatively correlated with overstorey tree canopy cover and litter cover.

5. These results indicate that population densities of AM fungi can rapidly increase following restoration treatments in northern Arizona ponderosa pine forests. This has important implications for restoring the herbaceous understorey of these forests because most understorey plants depend upon AM associations for normal growth. These results also can be applied to other ecosystems that are in a state of restoration or where the role of fire is just beginning to be understood.

INTRODUCTION

Prior to Euro-American settlement in the 1880s, ponderosa pine *Pinus ponderosa* Dougl. ex Laws. forests in the American Southwest were characterized by herbaceous understories dominated by grasses intermixed with large trees (Cooper 1960). Low intensity grass-fuelled fires every 2-20 years played a major role in determining the structure, composition, and stability of these ecosystems (Fulé, Covington & Moore 1997). Euro-American settlers drastically changed these forest ecosystems through heavy livestock grazing, intensive logging of old-growth trees, and fire suppression. Today these forests are often characterized by a large number of small trees with closed canopies, deep deposits of dead organic material on soil surfaces, and little herbaceous understorey. Efforts are currently underway to reverse structural and functional ecosystem changes caused by historical land management practices. The aim is to restore ecosystem diversity by returning ponderosa pine forests to a more open savannah-like structure and reintegrating the natural disturbance regime of fire (Covington & Moore 1994). Tree thinning and prescribed burning are two major components of this restoration effort.

A major objective for ponderosa pine forest restoration is to increase herbaceous understorey diversity and production to levels that emulate reference conditions

(Covington *et al.* 1997). Mycorrhizae are a critical link between aboveground plants and the soil system, playing an important role in plant nutrition, nutrient cycling, and the development of soil structure (Allen 1991; Smith & Read 1997). Many tree species are highly dependent on ectomycorrhizal (EM) fungi (Mikola 1970) and most herbaceous plants are associated with arbuscular mycorrhizal (AM) fungi (Smith, Charvat & Jacobson 1998). Consequently, numerous researchers have suggested a relationship between the recovery time of disturbed ecosystems and the abundance of infective propagules of mycorrhizal fungi (Reeves *et al.* 1979; Allen & Allen 1980; Bentivenga & Hetrick 1991; Noyd, Pfleger & Russelle 1995, Gange, Lindsay & Ellis 1999). In addition, Perry *et al.* (1989) refer to the strong link between plants and the soil biota as the "bootstrapping hypothesis." This hypothesis suggests through close mutual interactions some ecosystems are able to literally pull themselves up by their own "bootstraps", thus creating conditions to allow the system to persist over time (Perry *et al.* 1989). These authors showed that mycorrhizae helped facilitate succession following natural wildfires, where different species of plants formed mutualistic relationships with the same fungi throughout succession in forests in the northwestern United States. Other studies suggest that the role of mycorrhizae in facilitating succession may be dependent on the nutrient status of soil (Allen & Allen 1990). Because ponderosa pines are strongly EM and many of the native understorey grasses and forbs are strongly AM, we predicted that densities of AM fungal propagules should increase and EM fungal propagules should decrease in response to restoration thinning and prescribed burning in ponderosa pine forests. The specific objectives of this study were to: 1) quantify the effect of restoration thinning, and thinning and prescribed burning on AM and EM fungal propagule densities; and 2) assess the relationships between mycorrhizal fungal propagule densities and plant community and soil properties.

METHODS AND MATERIALS

Experimental Design

This research was conducted at two sites: the Fort Valley Experimental Forest and adjacent areas near Flagstaff, Arizona (hereafter referred to as Fort Valley) and the Mt. Trumbull Resource Conservation Area northwest of Grand Canyon National Park, Arizona (hereafter referred to as Mt. Trumbull). Two experimental blocks were established during the summer of 1998 at Fort Valley and four experimental blocks were established during the summer of 1999 at Mt. Trumbull. Treatment stands, each ~ 16 hectares, were randomly assigned within each block. Treatments at Fort Valley were: (1) no thinning or burning (control); or (2) thinning to a low level of replacement trees based upon presettlement tree densities. Thinning treatments at Fort Valley received prescribed burning treatments following the sampling for this study during the summer of 2001. Treatments at Mt. Trumbull were randomly assigned the same two treatments with the addition of prescribed burning to thinning. Specific details of the thinning treatments at Fort Valley are outlined in Fulé *et al.* (2001a) and specific details of the thinning treatments at Mt. Trumbull are outlined in Fulé *et al.* (2001b). Twenty systematically located permanent plots were located in each stand at Fort Valley and Mt. Trumbull. At each of these permanent plots we sampled herbaceous understorey and overstorey tree composition and abundance, fuel loads, and tree canopy cover.

Soil Field Sampling

At Fort Valley, soil samples were randomly taken from 10 of the 20 systematically placed plots along a 50-m transect within each of the 4 stands (2 blocks x 2 treatments) in late May 1999, six months after thinning, and again in May 2000, eighteen months after thinning. At Mt. Trumbull soil samples were randomly taken from 10 of the 20 systematically placed plots along a 50-m transect within each of the 8 stands (4 blocks x 2 treatments) in late June 2000, five months after thinning and three months after burning. Two samples at 20 metres along each transect (one for the AM bioassay and one for the EM bioassay) were taken and placed immediately into 4 cm diameter x 20 cm diameter deep Conetainers (Stuewe and Sons, Inc., Corvallis, Oregon USA) for "bait-plant bioassays" (Brundrett & Abbott 1994). Soils were collected to a depth of 15 cm using a hand trowel. We took samples to this depth because AM fungal propagule densities are generally highest in the surface 15 cm (Smith & Walker 1981). A third sample was taken at the same location for soil chemical analyses. This sample was frozen until it was analyzed.

Vegetation Field Sampling

At Fort Valley, we recorded pretreatment data for the herbaceous understorey and overstorey tree composition and abundance, fuel loads, and tree canopy cover in 1998. Post-thinning treatment data were collected in 1999 and 2000. These data were not significantly different between the two years; therefore, only post-treatment data from 2000 is presented because it is further along the restoration trajectory. At Mt. Trumbull, we recorded pretreatment data for the herbaceous understorey and overstorey tree composition and abundance, fuel loads, and tree canopy cover in 1999. Post treatment data was collected in 2000.

We surveyed the herbaceous and shrub understorey community along the same 50-m transects where soil samples were collected for AM and EM bioassays and soil chemical analyses. Every 30 cm along the 50-m transect, for a total of 166 points, substrate (plant, litter, soil, wood, rock) was recorded. If the substrate was a plant, the species was identified and its height was recorded. We determined plant cover by dividing the number of plant hits by 166 points for each transect. Overstorey tree data was collected in 400 m^2 circular plots centred on each plot centre. Tree species and diameter at breast height (dbh, 1.37 m) were recorded for all live and dead trees greater than 1.37 m in height.

In addition, at the same 30 cm intervals along the 50-m transect, tree canopy cover and fire severity in areas treated with prescribed burning were recorded. We determined tree canopy cover by recording the presence or absence of a tree canopy from a vertical projection. Fire severity was determined based upon descriptions in the Western Regional Fire Monitoring Handbook (NPS, 1992). Areas with charred litter, duff (the fermentation and humus layers of the forest floor) and wood were recorded as lightly burned areas, areas with litter mostly consumed, duff deeply burned and wood recognizable were recorded as moderately burned areas, and areas with litter and duff consumed leaving white ash and soil often reddish were recorded as severely burned. We used a 15-m planar transect located in a random direction from the plot centre to measure forest floor litter and duff depths. Every 1.5 m, litter and duff were recorded following guidelines outlined in Brown (1974).

Laboratory Analysis

Bait-plant bioassays are designed to detect all types of viable mycorrhizal fungal propagules including spores, fragments of mycorrhizal roots and extraradical hyphae. This method quantifies total mycorrhizal fungi more accurately than direct counts of sporocarps, spores, or colonized root lengths (Brundrett & Abbott 1994, Johnson, O'Dell & Bledsoe 1999). We used a corn *Zea mays* bioassay to determine the relative amount of infective propagules of AM fungi and a ponderosa pine bioassay to determine the relative amount of infective propagules of EM fungi. Corn is mycotrophic with many species of AM fungi and grows rapidly and uniformly; these advantages outweigh the disadvantage of not using a native host plant (Johnson, O'Dell & Bledsoe 1999). Plants were placed in a greenhouse and watered every 3 days until they were harvested at 6 weeks. Because pine seedlings grow more slowly than corn seedlings, pine seedlings were harvested at 12 weeks to determine inoculum potential. Roots were carefully washed free from the soil and weighed. Following mycorrhizal analysis, roots were oven-dried at 70° C for 24 hours and then reweighed. Shoot lengths and dry root and shoot weights were also measured. Corn roots were prepared for AM analysis by cutting roots into 2.5 cm segments, taking a random subsample of the cut roots of a known mass, clearing roots in 5 percent potassium hydroxide, and then staining with trypan blue in lactoglycerin (Koske & Gemma 1990). The gridline intersect method using a dissecting microscope was used to measure the proportion of root length containing AM fungal structures: arbuscules, vesicles, coils, internal mycorrhizal hyphae and external mycorrhizal hyphae (Giovannetti & Mosse 1980). We measured pine roots for fungal propagule density through direct examination using a dissecting microscope to quantify the proportion of root tips colonized with EM fungi (Gehring & Whitham 1991). Root tips were classified either as a living or dead EM tip or a living or dead non-mycorrhizal tip. Different morphological types and colours were also recorded.

Soil Analysis

Soil samples from each transect were analyzed for pH, total N, total P and organic C at the Bilby Research Soil Analysis Laboratory, Flagstaff, Arizona. Soil pH was determined in a 1:1 slurry by pH meter. Total N and P was measured using a Kjeldahl digestion of the soil material followed with the analysis of N and P by automated colorimetry using a Technicon auto-analyzer (Parkinson & Allen 1975). Organic C was determined by loss on ignition. Samples were heated in crucibles for 24 hours in a muffle furnace at 425° C and organic matter was estimated from net weight loss.

Statistical Analysis

Multivariate analysis of variance (MANOVA) repeated measures was used to determine the effects of thinning-only on mycorrhizal propagule densities for data collected in 1999 and 2000 with time and treatment as the two main variables in the analysis. We used analysis of variance (ANOVA) for a randomized block design in SPSS version 8 (SAS Institute 1997) to determine the effect of thinning-only and thinning and prescribed burning on vegetation, soil properties, and the proportion of AM fungal structures for the 2000 data. ANOVA was also used to determine the effect of thinning and prescribed burning on mycorrhizal propagule densities. Significance for analysis of variance tests was accepted at alpha ≤ 0.05. The Shapiro Wilks test was used to test data for normality and Leven's test was used to test for homogeneity of the variance (Milliken & Johnson 1984). Root infection data were angular transformed prior to analysis. Herbaceous plant abundance, graminoid cover, and soil properties were

square root transformed to improve normality and homoscedasticity assumptions (Zar 1984). Multiple regression was used to determine the relationship between infectivity and plant and community properties. Simple correlation analysis was used to determine the relationship between root infectivity and bait plant characteristics (length and weight).

RESULTS

Stand Characteristics

Pretreatment, there were no significant differences between control and treatment stand data for vegetation and site characteristics at the Fort Valley study site (1998) or at the Mt. Trumbull study site (1999) (Tables 4 & 5). Following thinning treatments, there were significantly less trees per hectare and tree canopy cover in the thinned only and thinned and prescribed burned units than their respective controls (Tables 4 & 5). At the Fort Valley study site, there were approximately 182 trees/hectare in the thinned only units and 1426 trees per hectare in the paired controls. At the Mt. Trumbull study site, there were approximately 336 trees per hectare in thinned and prescribed burn units compared with 1298 trees per hectare in the paired controls. Although the average herbaceous cover tended to be higher in treated units than in control units, the differences were not significant (Table 4). The herbaceous plant communities in the experimental units at Fort Valley were dominated by graminoids followed by non-legume forbs, legumes, and woody shrubs. Similar abundance patterns were present at Mt. Trumbull except there were more legumes than non-legume forbs. Sedges, *Carex* spp., dominated the herbaceous cover for both study sites along with C_3 (plant that produces a 3-carbon molecule during photosynthesis) grasses, including squirreltail *Elymus elymoides* (Rafinesque) Swezey and muttongrass *Poa fendleriana* (Steudel) Vasey. Mountain muhley *Muhlenbergia montana* (Nuttall) Hitchcock was the only abundant C_4 (plant that produces a 4-carbon molecule during photosynthesis) grass in the experimental units at Fort Valley and it was consistently less common than the abundant C_3 grasses. There were no abundant C_4 grasses in the experimental units at Mt. Trumbull.

Approximately 21 per cent of the area remained unburned following prescribed burning at Mt. Trumbull (Table 6). Of the area that burned, approximately 20 per cent was lightly burned, 38 percent was moderately burned, and 21 per cent was severely burned. There were no significant differences between soil properties in the treated and control units (Table 7). However, at both sites, organic C and total N levels appeared to be higher in both treated units in comparison with their paired controls and total P was slightly higher in the thinned and prescribed burned units at Mt. Trumbull than their controls, although none of these differences were statistically significant.

Mycorrhizal Infectivity

Mycorrhizal fungi colonized all bait-plants and colonization levels were influenced by restoration treatments at both sites. At Fort Valley infective propagule densities of AM fungi were significantly higher in the thinned units than their paired controls for both study years (Tables 1 & 2). Infective propagule densities of AM fungi at Mt. Trumbull were significantly higher in soils from the thinned and prescribed burned units in comparison with their paired controls ($F=39.13$, $P=0.008$; Table 3). Corn bioassay plants grown in the Fort Valley thinned only soils had significantly more vesicles and less hyphae than corn grown in their paired control soils ($F=2.1601$, $P=0.05$; $F=5.4437$, $P=0.001$; Figure 1a.) whereas there was no difference between the relative proportion of AM fungal structures in the Mt. Trumbull thinned and prescribed burned

soils and their controls (Figure 1b). Unlike the AM fungi, there was no significant difference in the relative amount of infective propagules of EM fungi in samples collected from treated units in comparison with their controls for 1999 or 2000 at Fort Valley (Tables 1 & 2) or at Mt. Trumbull in 2000 ($F= 1.077$ $P=0.3394$; Table 3). Sparsely branched bifurcated tips were the dominant EM morphotype for all stands.

AM colonization of the corn bait plants was not correlated with corn shoot weight or corn root weight ($r^2= -0.037$ and $r= 0.031$, $P \leq 0.05$). EM colonization of the pine bait plants was not correlated with pine shoot weight ($r^2= 0.11$, $P=0.74$) but was positively correlated with pine root weight ($r^2= 0.28$, $P=0.04$). For all 14 study units combined, about 85% of the variance of AM infectivity was explained by graminoid cover (square root cover) and tree canopy cover ($F= 13.12$ $P=0.0009$; Table 8). In contrast, for all study units combined, trees per hectare, tree canopy cover, or litter cover did not explain the variance of EM infectivity ($F=0.101$, $P=0.9573$; Table 8).

DISCUSSION

During the first two years, restoration treatments had no significant effect on the overall cover of herbaceous AM plants, even though plant cover did increase in the restoration treatments. AM abundance was highly correlated with grass cover and therefore areas with higher grass cover (restoration treatments) also had higher propagule densities of AM fungi. Contrary to our expectations, restoration treatments did not change EM propagule densities, illustrating that even though their host plant density was significantly reduced, EM fungi are able to maintain viable propagules for at least two years following thinning and one year following thinning and prescribed burning. Other studies have shown variable affects of tree thinning on EM fungal densities, depending on the disturbance intensity. For example, clearcutting a Douglas-fir *Pseudotsuga menziesii* (Mirb.) Franco forest in western Montana significantly reduced the number of EM roots and affected adjacent uncut stands for at least 7.6 m into the stand (Harvey, Jurgensen & Larsen 1980). In contrast, predisturbance population densities of EM fungi were maintained for 2 years after clearcutting an aspen *Populus tremuloides* Michaux stand (Visser *et al.* 1998). Prescribed fire also has varied effects on EM fungi, ranging from dramatic reductions in propagule densities and diversity after intense wildfires (Visser, Maynard & Danielson 1995), to no significant changes (Baar *et al.* 1999). A study of a low intensity wildfire showed little change in EM fungal composition or densities (Jonsson *et al.* 1999). This study suggested that if the organic layer, where EM mycelia are concentrated, remains largely undamaged, then fire would have little or no impact on EM fungi. This explanation may account for the lack of changes in EM fungal propagule densities to restoration thinning and thinning and prescribed burning in this study or there may have been a shift in the source of inoculum or species composition that we were unable to detect. Some studies have detected spores and sclerotia as the dominant inoculum-types following burning and there is a shift at a high taxonomic level from basidiomycetes to ascomycetes post fire (Baar *et al.* 1999; Grogan, Baar & Bruns 2000).

In contrast to EM fungi, AM fungi responded rapidly to restoration treatments in northern Arizona pine forests. Propagule densities of AM fungi significantly increased by an average of 20 percent in thinned-only, and in thinned and burned units compared with control units. Two main processes control population densities of mycorrhizal fungi

following disturbance: immigration of new propagules from nearby areas and survival and spread of residual propagules (Warner, Allen & MacMahon 1987). Rapid colonization of AM fungi has been illustrated in other studies. Gould *et al.* (1996) found that AM propagule densities increased significantly within 9 months of mining reclamation and increased 10-fold the following spring after seeding. Similarly, Johnson and McGraw (1988) found that taconite tailings that were initially devoid of AM fungi were colonized within weeks of reclamation seeding. It was hypothesized that spores were transferred to the reclaimed tailings by both biotic (animals) and abiotic (wind and water) vectors (Johnson & McGraw 1988).

In the present study, it is likely that AM fungi spread from pre-existing mycorrhizal hyphae in living and dead plant roots. These live and dead root systems and their mutualistic mycorrhizal associations represent the mechanism for the "bootstrapping hypothesis" (Perry *et al.* 1989). The persistence of these associations under unrestored conditions (dense, closed forest canopies and high fuel loads) and their ability to respond rapidly to tree removal and prescribed fire, suggests that AM associations may facilitate succession of this community to its previous dominance of herbaceous AM hosts. A study by Kovacic *et al.* (1984) found that AM hosts and AM fungal abundance were significantly higher in mountain pine beetle *Dendroctonus ponderosae* Hopk. killed ponderosa pine stands than under live ponderosa pine stands in northern Colorado. While mountain pine beetle outbreaks can be of epidemic proportions, their outcome in reducing live tree stand densities promotes changes in belowground AM fungal densities and aboveground herbaceous production. Other studies in different ecosystems have also shown changes in AM propagule densities with changes in tree densities. A successional study of AM propagule densities across a grassland to forest chronosequence showed AM inoculum potential increased with increasing grass cover and decreased in later successional sites with EM trees (Johnson *et al.* 1991). Similarly, a study by Benjamin *et al.* (1989) illustrated that herbaceous plants had lower AM colonization as tree density and shading increased, possibly because these plants had insufficient photosynthetic capability to support AM infection.

Soil disturbance has been reported to generally reduce AM propagule densities due to the destruction of the hyphal network during the break-up of the soil macrostructure (Reeves *et al.* 1979; Fairchild & Miller 1988). Consequently, one might predict that propagule densities should decrease following tree thinning, due to soil disturbance from mechanized logging equipment. This effect was not observed in our study, which indicates that either soil disturbance was not severe enough to have destroyed AM fungal propagules, that the sites were rapidly colonized by AM fungal spores and residual hyphae, or that the bioassay method may have missed any reduction. Because sunlight and photosynthetic capacity is greater in thinned stands, herbaceous host root densities probably increased with tree removal, which in turn would allow the herbaceous plant community to support more hyphae. Rives *et al.* (1980) also found no reduction in population densities of AM fungi following soil disturbance. It has been suggested that AM propagule densities in seasonal grasslands may be relatively tolerant of disturbance because their AM fungal communities produce high densities of perennating spores (Jasper, Abbott & Robson 1991).

Prescribed fire has variable effects on AM propagule densities ranging from decreased AM propagule densities (Klopatek, Debano & Klopatek 1988; Dhillion &

Anderson 1993), to no change (Anderson & Menges 1997; Rashid *et al.* 1997), to increases in AM propagule densities (Bentivenga & Hetrick 1991). Similar to soil disturbance, the effect of prescribed fire on AM propagules is highly dependent on the disturbance intensity. Because fire intensity can span three orders of magnitude (Pyne, Andrews & Laven 1996), soil is not heated uniformly during prescribed burns and therefore soil samples from burned areas are likely to contain highly variable levels of AM fungi, making the assessment of fire on AM fungi difficult. In our study, similar variance in the inoculum potential of soils from thinned-only and thinned-burned units suggest that these forests were not significantly affected by prescribed fire, which were mostly low intensity burns of short duration. Approximately 40% of the Mt. Trumbull study area was lightly burned or remained unburned following the prescribed fire and approximately 38% was only moderately burned. At the Fort Valley study site, a stand that was treated with thinning and a low intensity burn of short duration showed a 22% increase in AM propagule densities similar to the increases found at Mt. Trumbull (J. E. Korb, unpublished data). In contrast, high intensity burns of long duration in slash pile burning at the Fort Valley study site significantly reduced AM propagule densities by 98% (Korb 2001). Simulated laboratory fires have shown that heating field soil above 80° C almost completely eliminates AM fungi (Pattinson *et al.* 1999). Understanding the maximum soil temperature and duration that AM fungi can withstand at different soil depths will be crucial to understanding the effects of prescribed fire on AM fungi propagule densities in southwestern ponderosa pine forest restoration.

IMPLICATIONS FOR RESTORATION

Some evidence suggests that ponderosa pine understorey communities prior to the mid-1880s were dominated by warm-season (C_4) grasses, which are often strongly mycotrophic (Cooper 1960; Pearson, Mann & Howard 1971; Wilson & Hartnett 1998). However, current ponderosa pine forests are dominated by species that often form no mycorrhizal associations (e.g. *Carex geophila*) or C_3 grasses that are often weakly mycotrophic (Wilson & Hartnett 1998). These forests will probably continue to lack productive understorey communities, unless treatments are implemented that favour herbaceous host plants and AM fungi by reducing tree canopy cover and litter cover. Noyd *et al.* (1995) demonstrated that strongly mycotrophic C_4 grasses, big bluestem *Andropogon gerardii* Vitman and little bluestem *Schizachyrium scoparium* (Michaux) Nash, were unable to grow or survive as seedlings in soil where AM fungi were eliminated, but establishment of the C_3 grass Canada wild rye *Elymus canadensis* L. was unaffected by AM fungi availability. Similarly, Hetrick *et al.* (1994) found that C_4 grasses were competitively superior to C_3 grasses when grown in the presence of AM fungi, but C_3 grasses were competitively superior in soils without AM fungi. As a result, one can predict that increased populations of AM fungi in the thinned only and thinned and prescribed burned restoration stands may assist in the replacement of weakly mycotrophic species by strongly mycotrophic species, thereby increasing C_4 grass cover and leading to the maintenance of mycorrhizal compatible species (Francis & Read 1994; Johnson 1998).

Enhancing AM propagules does not always result in a favorable community as shown in a study by Marler et al. (1999) where AM fungi enhanced the competitive superiority of spotted knapweed *Centaurea maculosa* Lam. over a native bunchgrass. In

addition, our results suggest that restoration thinning may have caused a shift in the species composition of the AM fungal community at the Fort Valley study site where taxa that form abundant vesicles increased in the thinned treatments, while they did not increase at the Mt. Trumbull study site even though the proportion of vesicles in the controls at these two sites were similar. These changes in AM species may directly influence aboveground plant community composition and structure, because taxa of AM fungi differ greatly in their effects on plant fitness. Specifically, species of the Gigasporaceae family do not form vesicles and therefore an increase in vesicles could suggest a reduction in AM species of this taxon or an increase in other species that do readily form vesicles. Future studies of AM in ponderosa pine restoration areas will require analysis of the species composition of the fungal communities to determine if a shift in the fungal community is occurring in response to restoration treatments and whether these shifts impact the plant community composition.

Recent research in a variety of environments has shown that mycorrhizal interactions may be important determinants of plant diversity, ecosystem variability, and productivity (Hartnett & Wilson 1999; van der Heijden *et al.* 1998a,b; Klironomos *et al.* 2000). Host plant species composition influences AM fungal species composition (Johnson, Tilman & Wedin 1992; Bever *et al.* 1996; Eom, Hartnett & Wilson 2000), which provides evidence for current feedback models between soil communities and plant community structure (Bever *et al.* 1997). Future studies of ponderosa pine restoration treatment areas are needed to more fully understand responses of AM fungal communities and assess feedbacks between AM fungal and plant communities. Our results indicate that AM propagule densities respond rapidly to thinning and prescribed burning in southwestern ponderosa pine restoration treatments. This has important implications for land managers trying to restore the herbaceous understorey of these forests, because most understorey plants depend upon AM associations for normal growth.

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REFERENCES

Allen, E.B. & Allen, M.F. (1980) Natural re-establishment of vesicular-arbuscular mycorrhizae following strip mine reclamation in Wyoming. *Journal of Applied Ecology*, **17**, 139-147.

Allen, E.B. & Allen, M.F. (1990) The mediation of competition by mycorrhizae in successional and patch Environ. *Perspectives on Plant Competition* (eds J.B. Grace & G.D. Tilman), pp. 367-389. Academic Press, New York, USA.

Allen, M.F. (1991) *The Ecology of Mycorrhizae.* Cambridge University Press, New York, USA.

Anderson, R.C. & Menges, E.S. (1997) Effects of fire on sandhill herbs: nutrients, mycorrhizae, and biomass allocation. *American Journal of Botany*, **84**, 938-948.

Baar, J., Horton, T.R., Kretzer, A.M. & Bruns, T.D. (1999) Mycorrhizal colonization of *Pinus muricata* from resistant propagules after a stand -replacing wildfire. *New Phytologist*, **143**, 409-418.

Benjamin, P.K., Anderson, R.C. & Liberta, A.E. (1989) Vesicular-arbuscular mycorrhizal ecology of little bluestem across a prairie-forest gradient. *Canadian Journal of Botany*, **67**, 2678-2685.

Bentivenga, S.P. & Hetrick, B.A.D. (1991) Relationship between mycorrhizal activity, burning, and plant productivity in tallgrass prairie. *Canadian Journal of Botany*, **69**, 2597-2602.

Bever, J., Morton, J., Antonovics, J. & Schultz, P. (1996) Host-dependent sporulation and species diversity of arbuscular mycorrhizal fungi in a mown grassland. *Journal of Ecology,* **84,** 71-82.

Bever, J., Westover, K. & Antonovics, J. (1997) Incorporating the soil community into plant population dynamics: the utility of the feedback approach. *Journal of Ecology,* **85,** 1-13.

Brown, J.K. (1974) *Handbook for inventorying downed woody material.* United States Department of Agriculture Forest Service General Technical Report INT-16, Intermountain Forest and Range Experiment Station, Ogden, UT.

Brundrett, M.C. & Abbott, L.K. (1994) Mycorrhizal fungus propagules in the jarrah forests. I. Seasonal study of inoculum levels. *New Phytologist,* **127**, 539-546.

Cooper, C.F. (1960) Changes in vegetation, structure, and growth of southwestern pine forest since white settlement. *Ecological Monographs,* **30**, 129-164.

Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S. S. & Wagner, M.R. (1997) Restoring ecosystem health in ponderosa pine forests of the southwest. *Journal of Forestry,* **95**, 23-29.

Covington, W.W. & Moore, M. M. (1994) Southwestern ponderosa forest structure: changes since Euro-American settlement. *Journal of Forestry,* **92,** 39-47.

Dhillion, S.S. & Anderson, R. C. (1993) Seasonal dynamics of dominant species of arbuscular mycorrhizae in burned and unburned sand prairies. *Canadian Journal of Botany,* **71**, 1625-1630.

Eom, A-H, Hartnett, D. C. & Wilson, G.W.T. (2000) Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairies. *Oecologia*, **122**, 435-444.

Fairchild, G.L. & Miller, M.H. (1988) Vesicular-arbuscular mycorrhizas and the soil-disturbance-induced reduction of nutrient absorption in maize. *New Phytologist*, **110**, 75-84.

Francis, R. & Read, D. J. (1994) The contributions of mycorrhizal fungi to the determination of plant community structure. *Plant and Soil,* **159**, 11-25.

Fulé, P.Z., Waltz, A.E.M., Covington, W.W. & Heinlein, T.A. (2001a) Measuring forest restoration effectiveness in hazardous fuels reduction. *Journal of Forestry*, **99**, 24-29.

Fulé, P.Z., McHugh, C., Heinlein, T. A. & Covington, W. W. (2001b) Potential fire behavior is reduced following forest restoration treatments. *Ponderosa Pine Ecosystems Restoration and Conservation: Steps Toward Stewardship Proceeding* (eds Vance, G.K., Covington, W.W. & Edminster, C.B.), RMRS-P-22. pp. 28-35. Ogden, Utah. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Fulé P.Z., Covington W. W. & Moore, M. M. (1997) Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications,* **7**, 895-908.

Gange, A.C., Lindsay, D.E. & Ellis, L.S. (1999) Can arbuscular mycorrhizal fungi be used to control the undesirable grass *Poa annua* on golf courses? Journal of Applied *Ecology*, **36**, 909-919.

Gehring, C.A. & Whitham, T.G. (1991) Herbivore-driven mycorrhizal mutualism in insect-susceptible pinyon pine. *Nature,* **353**, 556-557.

Giovannetti, M. & Mosse, B. (1980) An evaluation of techniques for measuring vesicular-arbuscular mycorrhiza infection in roots. *New Phytologist,* **84**, 489-500.

Gould, A.B., Hendrix, J.W. & Ferriss, R.S. (1996) Relationship of mycorrhizal activity to time following reclamation of surface mine land in western Kentucky. 1. Propagule and spore population densities. *Canadian Journal of Botany,* **74**, 247-261.

Grogan, P, Baar, J. & Bruns, T.D. (2000) Below-ground ectomycorrhizal community structure in a recently burned bishop pine forest. *Journal of Ecology*, **88**, 1051-1062.

Hartnett, D.C. & Wilson, G.W.T. (1999) Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology*, **80**, 1187 -1195.

Harvey, A.E., Jurgensen, M.F. & Larsen, M.J. (1980) Clearcut harvesting and ectomycorrhizae: survival of activity on residual roots and influence on a bordering forest stand in western Montana. *Canadian Journal of Forest Research,* **10**, 300-303.

Hetrick, B.A.D., Hartnett, D.C., Wilson, G.W.T. & Gibson, D.J. (1994) Effects of mycorrhizae, phosphorus availability, and plant density on yield relationships among competing tallgrass prairie grasses. *Canadian Journal of Botany,* **72**, 168-176.

Jasper, D.A., Abbott, L.K. & Robson, A.D. (1991) The effect of soil disturbance on vesicular-arbuscular mycorrhizal fungi in soils from different vegetation types. *New Phytologist,* **118**, 471-476.

Johnson, N.C. (1998) Responses of *Salosa kali* and *Panicum virgatum* to mycorrhizal fungi, phosphorus and soil organic matter: implications for reclamation. *Journal of Applied Ecology,* **35**, 86-94.

Johnson, N.C., O'Dell, T. E. & Bledsoe, C. S. (1999) Methods for ecological studies of mycorrhizae (eds G.P. Robertson, C.S. Bledsoe, D.G. Coleman, & P. Sollins)

Standard soil methods for long-term ecological research. pp.378-411. Oxford University Press, New York, USA.
Johnson, N.C., Tilman, D. & Wedin, D. (1992) Plant and soil controls on mycorrhizal fungal communities. *Ecology*, **73**, 2034-2042.
Johnson, N.C., Zak, D.R., Tilman, D. & Pfleger, F.L. (1991) Dynamics of vesicular-arbuscular mycorrhizae during old field succession. *Oecologia,* **86**, 349-358.
Johnson, N.C. & McGraw, A.C. (1988) Vesicular-arbuscular mycorrhizae in taconite tailings. I. Incidence and spread of endogeonaceous fungi following reclamation. *Agriculture, Ecosystems and Environment,* **21**, 135-142.
Jonsson, L., Dalhberg, A., Nilsson, M.-C., Zackrisson, O. & Kårén, O. (1999) Ectomycorrhizal fungal communities in late-successional boreal forests, and their composition following wildfire. *Molecular Ecology,* **8**, 205-215.
Klironomos, J.N., McCune, J., Hart, M. & Neville, J. (2000) The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity. *Ecology Letters,* **3**, 137-141.
Klopatek, C.C., Debano, L.F. & Klopatek, J.M. (1988) Effects of simulated fire on vesicular-arbuscular mycorrhizae in pinyon-juniper woodland soil. *Plant and Soil,* **109**, 245-249.
Korb, J.E. (2001) *Plant community dynamics in southwestern ponderosa pine forest restoration.* PhD thesis, Northern Arizona University.
Koske, R.E. & Gemma, J.N. (1990) VA mycorrhizae in strand vegetation of Hawaii: evidence for long-distance codispersal of plants and fungi. *American Journal of Botany,* **77**, 466-474.
Kovacic, D.A., St. John, T. V. & Dyer, M.I. (1984) Lack of vesicular-arbuscular mycorrhizal inoculum in a ponderosa pine forest. *Ecology,* **65**, 1755-1759.
Marler, M.J., Zabinski, C. A. & Callaway R.M. (1999) Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. *Ecology,* **80**, 1180-1186.
Mikola, P. (1970) Mycorrhizal inoculation in reforestation. *International Review of Forest Research,* **3**, 123-196.
Milliken, G.A. & Johnson, D.E. (1984) *Analysis of messy data, Vol. I. Designed experiments.* Van Nostrand Reinhold Co., New York.
National Park Service (1992) *Western Region Fire Monitoring Handbook.* USDI National Park Service, Western Region, San Francisco CA.
Noyd, R.K., Pfleger, F. L. & Russelle, M.P. (1995) Interactions between native prairie grasses and indigenous arbuscular mycorrhizal fungi: implications for reclamation of taconite iron ore tailing. *New Phytologist*, **129**, 651-660.
Parkinson, J.A. & Allen, S.E. (1975) A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. *Community Soil Science and Plant Analysis,* **6**, 1-11.
Pattinson, G. S., Hammill, K.A., Sutton, B.G. & Mcgee, P.A. (1999) Simulated fire reduces the density of arbuscular mycorrhizal fungi at the soil surface. *Mycological Research,* **103,** 491-496.
Pearson, H.A., Mann, J.F. & Howard, D.A. (1971) Timing use of cool- and warm season grasses on pine ranges. *Journal of Range Management*, **24**, 162-163.

Perry, D.A., Amaranthus, M.P., Borchers, J.G., Borchers, S.L. & Brainerd, R.E. 1989. Bootstrapping in ecosystems. *BioScience,* **39**, 230-237.

Pyne, S.J., Andrews, P.L. & Laven, R.D. (1996) *Introduction to Wildland Fire 2nd Edition.* John Wiley and Sons, Inc, New York.

Rashid, A. Ahmed, T., Ayub, N. & Khan, A.G. (1997) Effect of forest fire on number, viability and post-fire re-establishment of arbuscular mycorrhizae. *Mycorrhiza,* **7**, 217-220.

Reeves, F.B., Wagner, D., Moorman, T. & Kiel, J. (1979) The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. *American Journal of Botany,* **66**, 6-13.

Rives, C.S., Bajwa, M. I., Leberta, A.E. & Miller, R.M. (1980) Effects of topsoil storage during surface mining on the viability of VA mycorrhizae. *Soil Science,* **129**, 253-257.

Smith, M.R., Charvat, I. & Jacobson, R.L. (1998) Arbuscular mycorrhizae promote establishment of prairie species in a tallgrass prairie restoration. *Canadian Journal of Botany,* **76**, 1947-1954.

Smith, S.E. & Read, D.J. (1997) *Mycorrhizal symbiosis—2nd edition.* Academic Press, San Diego.

Smith, S.E. & Walker, N.A. (1981) A quantitative study of mycorrhizal infection in Trifolium: separate determination of the rates of infection and of mycelial growth. *New Phytologist,* **89**, 225-240.

van der Heijden, M.G.A., Boller, T., Wiemken, A. & Sanders, I.R. (1998a)Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. *Ecology,* **79**, 2082-2091.

van der Heijden, M.G.A., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, P., Boller, T., Wiemken, A. & Sanders I.R. (1998b) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature,* **395**, 69-72.

Visser, S., Maynard, D. & Danielson, R.M. (1998) Response of ecto- and arbuscular mycorrhizal fungi to clear-cutting and the application of chipped aspen wood in a mixed wood site in Alberta, Canada. *Applied Soil Ecology,* **7**, 257-269.

Visser, S. (1995) Ectomycorrhizal fungal succession in jack pine stands following wildfire. *New Phytologist,* **129**, 389-401.

Warner, N.J., Allen, M.F. & MacMahon, J.A. (1987) Dispersal agents of vesicular-arbuscular mycorrhizal fungi in a disturbed arid ecosystem. *Mycologia,* **79**, 721-730.

Wilson, G.W.T. & Hartnett, D.C. (1998) Interspecific variation in plant responses to mycorrhizal colonization in tallgrass prairie. *American Journal of Botany,* **85**, 1732-1738.

Zar, J.H. (1984) *Biostatistical analysis, 2nd ed.* Prentice-Hall. Englewood Cliffs, New Jersey, USA.

Figure 1a-b. The proportion of different AM fungal structures within colonized corn roots grown in soils collected from **(a)** the Ft. Valley thinned only and paired control units and **(b)** the Mt. Trumbull thinned and prescribed burned and pair control units. Values indexed by different letters are significantly different at the $P \leq 0.05$ between treatments.

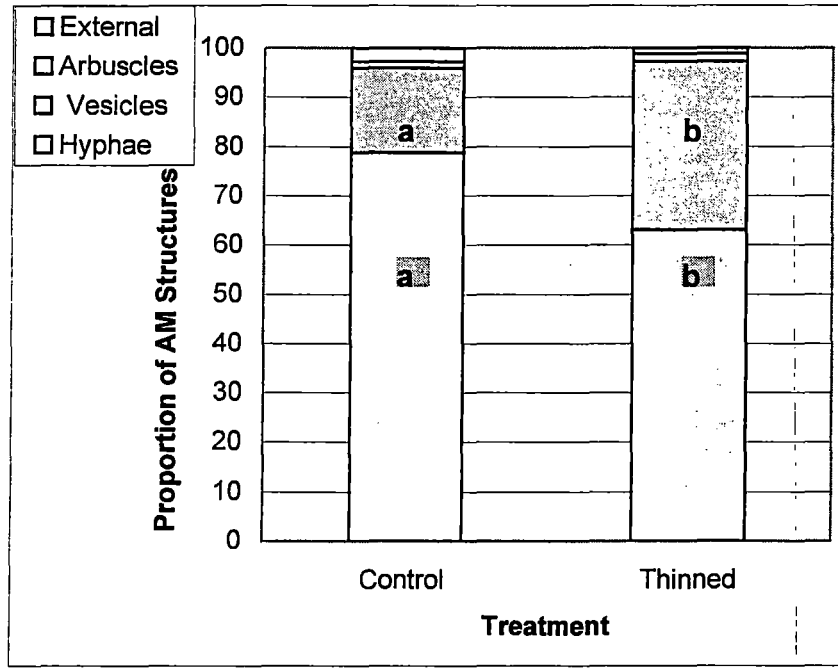

Figure 1a.

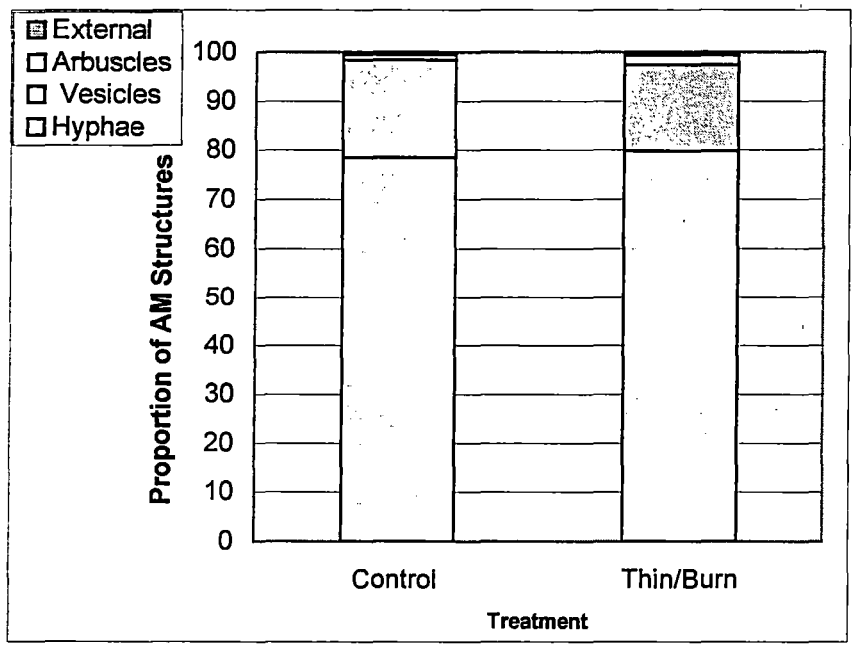

Figure 1b.

Table 1. The relative amount of mycorrhizal propagules indicated by the percentage of the corn root length colonized with AM and the percentage of EM root tips in ponderosa pine bait-plant bioassays from the Ft. Valley thinned-only and paired control units in 1999, six months after thinning, and 2000, eighteen months after thinning. Data are expressed as means (N=2) ± SEM.

Mycorrhizae	Control		Treatment	
Type	1999	2000	1999	2000
AM % colonized	21.28 ± 3.1	18.26 ± 4.4	44.6 ± 4.3	39.05 ± 4.6
EM % colonized	31.42 ± 2.7	34.77 ± 2.6	33.68 ± 3.1	37.0 ± 2.9

Table 2. F-ratios from MANOVA tests of the effects of treatment from the Ft. Valley thinned-only and paired control units and time, six months after thinning and eighteen months after thinning for the relative amount of AM propagules and EM root tips. Data were analyzed on angular transformed data. Exact *P* values are provided in parentheses.

	Source of variation			
	Treatment	Time	Treatment x Time	df
AM % colonized	15.05 (.0605)	6.78 (.1211)	0.0097 (.9305)	3
EM % colonized	1.72 (.3198)	0.697 (.4927)	1.01 (.4199)	3

Table 3. The relative amount of mycorrhizal propagules indicated by the percentage of the corn root length colonized with AM and the percentage of EM root tips in ponderosa pine from bait-plant bioassays from the Mt. Trumbull thinned and prescribed burned, and paired control units for 2000, five months after thinning and three months after burning. Differences between the units were determined by ANOVA on angular transformed data. Data are expressed as means (N=4) ± SEM. Transformed data are presented in parentheses.

Mycorrhizae Type	Control	Treatment	*P*	df
AM (% colonized)	17.75 ± 1.94 (0.3425 ± 0.027)	36.63 ± 5.4 (0.578 ± 0.026)	.008	7
EM (% colonized)	32.82 ± 2.78 (0.576 ± 0.022)	34.73 ± 2.18 (0.606 ± 0.021)	.3394	7

Table 4. Vegetation and site characteristics for the Ft. Valley control and thinned units for pretreatment 1998 data and post-treatment 2000 data. Data are expressed as means (N=2) ± SEM. Herbaceous cover data was square root transformed prior to analysis.

	Pretreatment 1998		Post-treatment 2000	
Variable	Control Stand	Treatment Stand	Control Stand	Treatment Stand
trees/hectare	1415.1 ± 392	1162 ± 141.4	1426.2 ± 330 a	182.3 ± 34 b
tree canopy cover (%)	62.37 ± 5.5	57.61 ± 3.8	61.03 ± 4.41 a	34 ± 2.95 b
herbaceous cover (%)	9.67 ± 1.92	9.23 ± 1.2	9.06 ± 1.76	11.22 ± 1.4
Simpson's diversity index	2.92 ± .44	2.89 ± .38	2.88 ± .62	3.61 ± .46
litter load (kg/ha)	14211 ± 1508	14133.76 ± 1980	14363 ± 1508	15625 ± 2598
duff load (kg/ha)	25127 ± 2006	25338.22 ± 3266	25836 ± 3103	26379 ± 3266

Values indexed by a different letter are significantly different at the $P \leq 0.05$ level between paired control and treatment units for the same sampling year.

Table 5. Vegetation and site characteristics for the Mt. Trumbull control and thinned/prescribed burned units for pretreatment 1999 data and post-treatment 2000 data. Data are expressed as means (N=4) ± SEM. Herbaceous cover data was square root transformed prior to analysis.

	Pretreatment 1998		Post-treatment 2000	
Variable	Control Stand	Treatment Stand	Control Stand	Treatment Stand
trees/hectare	2128.47 ± 700.9	1866.67 ± 786.1	2193.1 ± 355 a	336.3 ± 119 b
tree canopy cover (%)	58.96 ± 5.8	53.15 ± 6.98	61.51 ± 5.73 a	33.49 ± 7.1 b
herbaceous cover (%)	6.54 ± 1.32	6.21 ± 1.52	6.13 ± 1.94	10.61 ± 5.26
Simpson's diversity index	2.26 ± .32	2.31 ± .26	2.43 ± .24	2.33 ± .43
litter load (kg/ha)	13873 ± 1204	13655 ± 1866	13500.23 ± 199 a	6169 ± 2393 b
duff load (kg/ha)	22985 ± 2877	23034 ± 3146	23239.7 ± 218 a	10100 ± 1760 b

Values indexed by a different letter are significantly different at the $P \leq 0.05$ level between paired control and treatment units for the same sampling year.

Table 6. Mean substrate burn severity for Mt. Trumbull thinned/prescribed burned units. Lightly burned areas had charred litter and duff, moderately burned areas had litter and duff mostly consumed, and severely burned areas have litter and duff consumed leaving white ash. N=4 ± SEM, 10 replicates in each block.

Severity Level	Mean (in percent)
Not Applicable (Rock)	4.6 ± 3.18
Not Burned	16.4 ± 7.77
Lightly Burned	19.4 ± 7.66
Moderately Burned	37.8 ± 11.15
Severely Burned	21.0 ± 5.35

Table 7. Post-treatment soil characteristics (pH, Organic C, Total N, Total P) for the Ft. Valley control and thinned units and the Mt. Trumbull control and thinned/prescribed burned units in 2000. Data are expressed as means (N=2) ± SEM at Ft. Valley, (N=4) ± SEM at Mt. Trumbull, 10 replicates in each block. All data was square root transformed prior to analysis.

	Fort Valley		Mt. Trumbull	
Variable	CT	T	CTB	TB
pH	5.74 ± .11	5.7 ± .11	6.4 ± .02	6.40 ± .07
C (% loss on ignition)	8.81 ± .63	10.75 ± 1.19	10.97 ± 1.05	12.03 ± 1.43
Total N (mg/Ng)	1.38 ± .1	1.61 ± .16	2.04 ± .17	2.27 ± .31
Total P (mg/Pg)	0.93 ± .05	0.91 ± .03	1.20 ± .14	1.47 ± .20

Treatments were: control for Ft. Valley thinned units (CT), Ft. Valley thinned units (T), Mt. Trumbull control for thinned/prescribed burned units (CTB), and Mt. Trumbull thinned/prescribed burned units (TB).

Table 8. Multiple regression analysis results for AM and EM infectivity and plant community characteristics for the six Ft. Valley study units and eight Mt. Trumbull study units combined. Graminoid cover was square root transformed prior to analysis.

Dependent variable and predictors	Coefficient	t	*P*	r^2	df	F	*P*
Multiple regressions							
AM infectivity				0.853	4,13	13.12	.0009
Constant	7.17	0.38	0.715				
Graminoid cover	15.53	3.05	0.014				
Tree canopy cover	-0.34	-2.5	0.034				
EM infectivity				0.029	3,10	0.101	0.9573
Constant	30.89	3.26	0.008				
Trees/hectare	.0004	0.18	0.861				
Tree canopy cover	-0.054	-0.46	0.655				
Litter cover	0.0804	0.52	0.617				

Slash pile burning affects on mycorrhizae, soil properties, and plant establishment: recommendations for amelioration

ABSTRACT

Understanding the effects of potential vector areas on non-native plant establishment and how these vectors can be ameliorated is critical to the maintenance of native biodiversity and ecosystem function. We investigated the effects of slash pile burning on biotic and abiotic soil properties and plant establishment and experimentally assessed methods to ameliorate slash pile scars. Thirty slash pile scars were studied in two *Pinus ponderosa* stands. Arbuscular mycorrhizal (AM) propagule densities, soil seed bank, and soil chemical properties were measured along fire intensity gradients across each scar. Five 1-m^2 plots were established in each scar to quantify effects of amelioration treatments on herbaceous plant growth and AM propagule densities. Slash pile burning nearly eliminated populations of viable seeds and AM propagules and altered soil chemical properties. Amending scars with native seeds increased the cover of native forbs and grasses. Furthermore, adding both seed and living soil more than doubled total native plant cover and decreased ruderal and exotic plant cover. This suggests that factors in living soil facilitate recovery of native plant communities.

INTRODUCTION

A major dilemma in forest management and restoration is the disposal of slash (tree crowns, bole tips, small boles). Land managers commonly gather unmarketable small diameter trees and slash into large piles near roads and burn them under appropriate weather conditions. Although slash pile scars only cover a small portion of forest ecosystems, they are problematic because they often act as vector areas for the spread and establishment of undesirable non-native and ruderal plants into the forest interior following thinning (Dickinson and Kirkpatrick 1987). Managing non-native species has been identified as a critical factor to maintaining native biodiversity and ecosystem function (Byers *et al.* 2002). Despite ample antidotal evidence of detrimental effects of slash pile scars, few quantitative studies have assessed these effects and no quantitative studies have been conducted to determine methods to ameliorate them.

Arbuscular mycorrhizal (AM) fungi are important mediators of plant community composition and structure (Gange *et al.* 1993; Hartnett and Wilson 1999; Jordan *et al.* 2000; Klironomos, 2002). These mutualistic fungi can improve plant establishment, nutrient uptake, drought tolerance, and protection from plant pathogens, and they may be necessary for reestablishing vegetation in severely disturbed soil environments (Gould *et al.* 1996). Studies show that AM fungal colonization (Schenck *et al.* 1975; Pattinson *et al.* 1999), spore densities, and species richness are reduced (Dhillon *et al.* 1988, Gibson and Hetrick 1988) in severely burned areas. Consequently, to increase establishment of native grasses and forbs in slash pile scars where AM fungi have been significantly reduced or eliminated it may be necessary to reinoculate AM fungi using amendments of unburned soil containing viable AM propagules. In addition, seed amendments may be necessary to increase the availability of viable native seeds following their destruction by fire.

We hypothesized that severely burned slash pile scars would have significantly reduced propagule densities of plants and AM fungi as well as altered soil properties. In addition,

we hypothesized that seed and soil amendments containing viable AM propagules would increase the establishment of native plants in severely burned slash pile scars. The specific objectives of this study were to: 1) determine the effect of slash pile burning on densities of viable plant and AM fungal propagules and soil properties; and 2) determine the effect of amelioration treatments on herbaceous plant establishment within burned slash pile scars. We found that burning slash eradicates plant and AM fungal propagules and alters soil properties, and that amending fire scars with native seed in conjunction with living soil is necessary to reestablish native herbaceous plant species richness and cover.

METHODS

Experimental Site and Design

This research was conducted in the Coconino National Forest near Flagstaff, Arizona, U.S.A. Our study sites were at 2250 m elevation in two adjacent ~16 hectare units that were thinned in the winter of 1999. Piles of slash created during tree thinning were burned in February 2000. Over 50 slash piles (averaging 9 m in diameter and 3 - 4 m tall) were created from the thinning treatments. Estimated total fuel mass consumed for each slash pile averaged between 1.4 and 3.2 metric tons (Hardy 1996). For this research, we randomly chose 30 slash piles of similar size to minimize variation in fire severity among piles.

Prior to thinning and prescribed burning, the vegetation at the study site consisted of pure ponderosa pine stands intermixed with perennial grasses and numerous forbs. Soils are moderately well-drained clays and clay loams derived from basalt and are classified as fine, montmorillonitic Typic Argiboroll (TESCNF, 1995). The A horizon extends only 10 cm deep and the remaining soil profile extends 114 to 152 cm depth before reaching the fractured basalt bedrock (Overby, 2002, personal communication). Precipitation occurs as snowfall and rain during the winter, a pronounced drought in May and June, and frequent monsoon rains in July and August. Average summer precipitation is 20.8 cm. Daily mean temperatures range from 5° to 17° C.

Fire Intensity Gradient

Boundaries of slash pile scares were clearly identified by white ash, charred, blackened soil, and no vegetation. Transects were established in a N-S direction across the boundaries of each of the 30 slash pile scars, with 3 m extending inside and 3 m outside the scar. We assumed that sampling points along these transects represent a fire intensity gradient with the hottest soil temperatures 3 m inside the scar and coolest 3 m outside the scar. Soil samples were collected along each transect in May 2000 and May 2001 (3 and 15 months after burning). Soils were collected to a depth of 15 cm using a hand trowel and immediately placed into 4 cm diameter x 20 cm deep Conetainers (Stuewe and Sons, Inc., Corvallis, Oregon, U.S.A.).

We used a *Zea mays* (*corn*) bait-plant bioassay to determine the relative amount of infective propagules of AM fungi in our soil samples. Bait-plant bioassays are designed to detect all types of viable mycorrhizal fungal propagules including spores, fragments of mycorrhizal roots and extraradical hyphae, and therefore more accurately quantify total densities of AM fungal propagules than direct counts of sporocarps, spores, or colonized root lengths (Brundrett and Abbott 1994). Corn seeds were sown in freshly collected soils and the plants were maintained in a greenhouse for 6 wk. Corn roots were cut into 2.5 cm segments and subsamples were cleared in 5 % KOH and stained with trypan blue

in lactoglycerin (Koske and Gemma 1990). Proportion of root length containing AM fungal structures (arbuscules, vesicles, coils, and hyphae) was measured by the gridline intersect method using a dissecting microscope (Giovannetti and Mosse 1980).
In May 2000, additional soil samples were collected along each transect using a 5 cm diameter metal core to a depth of 5 cm. Populations of viable seeds were assessed by placing these soil cores on top of 2 cm of sterilized soil in 11 x 11 cm plastic containers in an un-heated greenhouse (18°C – 30°C). Containers were watered daily using an automatic mist system. Over a 4 month period, plant seedlings that emerged were identified to species, counted, and removed. Containers of sterilized soil were also maintained without living soil cores to determine if there was any greenhouse contamination. Also in May 2000, soil samples for chemical analyses were collected to a depth of 10 cm using a hand trowel 3 m inside the scar, at the scar edge, and 3 m outside the scar. In October 2001, soil samples were collected 10 m outside the scar in addition to the other sampling locations to quantify KCl extractable ammonium-nitrogen (NH_4-N) and nitrate-nitrogen (NO_3-N).

Amelioration Experiment

Five 1-m^2 (0.5 m x 2 m) plots were randomly located within each slash pile scar at least 1 m from the scar edge and at least 1 m from each other and were randomly assigned one of five treatments: 1) no treatment (control); 2) living soil amendment (containing microorganisms, AM fungi, and plant propagules); 3) sterilized soil amendment (no propagules); 4) seed amendment; or, 5) seed/soil amendment. Topsoil that had recently been stockpiled from road construction 1 km from the experimental site was used for the soil amendments. A previous study showed high densities of viable AM propagules in this soil (Korb *et al.* 2001). Soil taken from the same location was steam sterilized for 48 h to create the sterilized soil amendment without living organisms but with the same chemical and physical properties as the living soil amendment. In June, 2000, treatments 2, 3, and 5 had 20,000 cm^3 of living or sterilized soil layered onto each 1 m^2 plot, resulting in an average amendment depth of 2 cm. When the amendment soil was collected, 20 soil cores were sampled to quantify populations of viable seeds using the procedures described previously.
In May 2001 (15 months following burning and 11 months after soil amendments were added) 15 cm deep soil samples were collected from the experimental plots in each slash pile scar to quantify AM propagule densities using bait-plant bioassays. In October 2001, soil samples were collected to a depth of 10 cm from the control, soil amendment, and seed/soil amendment to quantify KCl extractable NH_4-N and NO_3-N.
Seed amendments consisted of a mixture of 19 species of native grasses and forbs that were abundant in the extant vegetation surrounding the slash pile scars (Table 1). Seeds were purchased from the nearest possible regional source (Colorado Native Seed in Salida, Colorado U.S.A.). Purity of the seed was verified in greenhouse and field trials. Treatments 4 and 5 were sown with 8.4 g of grass seed and 2.8 g of forb seed per 1-m^2 plot, representing equal proportions of grasses and forbs by weight. Seeds were sown in early July 2000 (5 months after burning) to coincide with the monsoon rains in late summer and mimic treatments that could be implemented by land managers (i.e., no supplemental water). In September 2000 and in September 2001 (7 and 19 months after the piles were burned) all seedlings and mature plants in each of the plots were identified and counted. In addition, the cover of each plant species was determined using the ocular estimate method to the nearest 0.1 %.

Soil Analysis

Soil chemical properties were analyzed at the Bilby Research Soil Analysis Laboratory, Flagstaff, Arizona. Soil pH was determined in a 1:1 slurry using a pH meter. Total N and P were measured following Kjeldahl digestion by automated colorimetry using a Technicon auto-analyzer (Parkinson *et al.* 1975). Available NH_4-N and NO_3-N were determined from KCl extracts of freshly collected soil by automated colorimetry using a Technicon auto-analyzer (Parkinson *et al.* 1975). Organic C was determined by loss on ignition, samples were heated to 425° C for 24 h and organic matter was estimated from mass loss.

Statistical Analysis

Repeated measures multivariate analysis of variance (MANOVA) and analysis of variance (ANOVA) were used. The Shapiro Wilk test was used to test data for normality, and Leven's test was used to test for homogeneity of the variance (Zar 1984). Prior to analysis, some data were transformed to improve normality and homoscedasticity assumptions (Zar 1984). Root colonization data were arcsin square root transformed, soil seed bank densities and some individual plant species variables were log (x+1) transformed, and soil properties were square root transformed. Tukey's Honestly Significant Difference test was used to make multiple comparisons of means following a significant result. All analyses were performed using SPSS version 8 (SAS Institute 1997).

RESULTS

Fire Intensity Gradient

At both sampling dates, corn bait-plants grown in soils collected from inside the slash pile scars had significantly lower AM colonization than those grown in soils collected from the scar edges and 3 m outside the scars (Figure 1). Infective propagule densities of AM fungi were also significantly reduced at the scar edges in comparison to 3 m outside the scars. Between 3 and 15 months after burning, there was a significant increase in AM propagule densities at the scar edge and 3 m outside the scar but not in the interior of the slash pile scar (Figure 1).

In 2000, there were significantly more viable seeds 3 m outside the scars than 3 m inside the scars or at the scar edges (Figure 2). The majority of viable seeds were from exotic or ruderal species (native species that prefer disturbed, high nutrient habitats, Grime 1979). Three m outside the scar, the exotic seed bank was dominated by *Verbascum thapsus* L. (mullein), an early successional species of disturbed habitats, with a mean of 368 seeds/m^2. *Linaria dalmatica* (L.) P. Mill. (dalmation toadflax) accounted for the remaining exotic seed bank with 45 seeds/m^2.

Differences in soil chemical properties were evident across the fire intensity gradient. Soil pH was significantly higher 3 m inside the scars in comparison to the scar edges and 3 m outside the scars (Figure 3a). In contrast, total N and organic C were significantly higher 3 m outside the scars in comparison to the scar edges and 3 m inside the scars (Figures 3b-c). There was no significant difference in total P across the transects (Figure 3d). KCl extractable NH_4-N and NO_3-N were significantly higher 3 m inside the scar (7.92 mg/kg and 12.95 mg/kg, respectively) in comparison to the scar edge (3.94 mg/kg and 0.29 mg/kg, respectively) and 10 m outside the scar edge (4.1 mg/kg and 1.02 mg/kg, respectively) as determined by ANOVA, $p=0.05$.

Amelioration Experiment

Soils collected from control plots and plots amended with sterilized soil had significantly lower densities of infective AM propagules than soils from plots amended with both seed and soil 15 months following burning and 11 months after soil amendments were added to the slash pile scars (Figure 4). There was no significant difference in KCl extractable soil NH_4-N or NO_3-N between the control, sterilized soil amendment and seed/soil amendment plots (mean values were 9.7 mg/kg NH_4-N, and 14.1 mg/kg NO_3-N).

The live soil amendment contained an average of 256 viable seeds/m^2, with *Carex* spp. the most abundant species and *Muhlenbergia montana, Verbascum thapsus* and *Laennecia schiedeana* (Less.) Nesom (pineland marshtail) also common. During the first growing season in 2000 (7 months after burning and 2 months after seeding) only seeded forbs and grass species became established, and there was no natural regeneration of ruderals or exotics. Forb and graminoid cover was significantly higher in the seed/soil amendments than the seed amendments (Figures 5a-b). During the second growing season in 2001, native forb and graminoid cover was significantly higher in the seed amended plots than in the control, sterilized soil or soil amended plots but lower than plots amended with both seed and soil (Figures 5a-b). There was no significant difference in exotic plant cover between any of the amendment treatments, but the seed/soil amendments had the lowest exotic cover (Figure 5c). The most abundant exotic species was *Verbascum thapsus*. Other exotic species included *Cirsium vulgare* (Savi) Tenore (bull thistle), and *Linaria dalmatica.* Ruderal species had significantly higher cover in the control, sterile soil amendment, and soil amended plots than those amended with both seed and soil (Figure 5d). The most abundant ruderal species was *Laennecia schiedeana.*

Five of the seeded species did not germinate in any of the plots either growing season and four species only germinated during the second growing season (Table 1). Native grass cover was significantly higher for seeded *Bouteloua gracilis, Elymus elymoides,* and *Muhlenbergia wrightii* in plots amended with live soil and seed than seed only plots for 2000 and 2001 (Table 1). Similarly, native forb cover was significantly higher for seeded *Ipomopsis aggregata* and *Linum lewisii* in plots amended with live soil and seed than seed only plots for 2000 and 2001 and *Penstemon virgatus* and *Thermopsis divaricarpa* was significantly higher in plots amended with live soil and seed for 2001 (Table 1).

DISCUSSION

Slash pile burning leaves persistent scars on the land. We found that slash pile scars have significantly altered soil properties and virtually no viable plant seeds and AM propagules. Other studies also report loss of seed banks (Hassan and West 1986; Odion and Davis 2000) and viable AM propagules (Klopatek *et al.* 1988, Berch *et al.* 1993) following intense fire. Combustion of the litter and duff horizon along with soil heating during slash burning are most likely responsible for the low number of viable seeds (Moore and Wein 1977) and AM propagules in the scars that we studied. Maximum soil surface temperatures are usually 500 - 700° C during heavy slash burns in chaparral (Rundel 1983), and temperatures at 10 cm and 22 cm depth in mineral soil can reach over

250° C and 100° C respectively in pine (Roberts 1965). Within a growing season, populations of viable AM fungal propagules were recovering at the scar edge but not in the center of the scar. This corroborates other studies that show neutral or positive responses of AM activity following low intensity fires where AM hyphae most likely survive in roots of nearby plants (Rashid *et al.* 1997) or as propagules deeper in the soil profile where soil heating is not severe (Pattinson *et al.* 1999; Korb *et al.* 2001).

Slash pile burning also altered soil chemistry. Elevated soil pH within the scars was likely due to the hydrolysis of base cation oxides that are abundant in ash following severe burns (Fuller *et al.* 1955; Ballard 2000). Organic C and total soil N was significantly lower inside the scars suggesting that the intense fire volatilized C and N compounds (Klemmedson 1976; Weast 1988). Studies have shown that while burning may reduce total soil N immediately following a fire, NH_4-N often increases because of pyrolysis of forest floor material, and within a year NO_3-N also increases due to nitrification of the NH_4-N pulse (Covington *et al.* 1991, Ellingson *et al.* 2000). This pattern of elevated soil NH_4-N immediately following the fire and a subsequent increase in NO_3-N was observed in our study. Unlike N and Organic C, total soil P showed no significant response to slash pile burning. Because 94 - 98 % of soil P is located in the mineral soil layers and not in the litter layer, P is not as sensitive to severe burning as N (Neary *et al.* 1999).

Slash pile scars are problematic because they often remain unvegetated (Covington *et al.* 1991) or become colonized by exotic (frequently invasive) plant species (Dickinson and Kirkpatrick 1987). Consequently, we were interested in identifying restoration treatments that encourage the establishment of native plants and discourage colonization by exotic plants. Our amelioration experiment indicates that addition of both live soil and native seed generated the highest species richness and abundance of native plants and the lowest species richness and abundance of exotic and ruderal plants. Direct seeding on ash resulted in lower native species richness and less than half the native plant cover compared to plots amended with both seed and live soil. Also, exotic plant cover was significantly lower in plots receiving dual seed and soil amendments compared to those receiving only seeds. Areas amended with live soil and seed were more closely related to adjacent areas that had low severity burns than the other amendment treatments including seed only. On average, native plant cover in our live soil and seed amended plots in 2001 was 11.9 % cover, which is similar to native plant cover outside the slash piles (11.2 %) in areas that received tree thinning and a low severity burn, which represents an artificial "target" for native plant cover (Korb, unpublished data). Conversely, areas within the slash pile scar with no soil or seed amendment (control) had on average < 0.01 % native plant cover.

Plant community composition is clearly impacted by the presence and function of AM symbioses (van der Heijden *et al.* 1998; Hartnett and Wilson 1999; Klironomos 2002). Consequently, reintroduction of AM fungi in the living soil amendment may have facilitated the success of the seed/soil treatments. Propagule densities of AM fungi were higher in the seed/soil treatment than in any of the other treatments. Other studies have found that AM fungi can promote the establishment of native plant cover in disturbed habitats (Gange *et al.* 1990, Smith *et al.* 1998) and that AM fungal propagule densities will remain low in severely disturbed soil environments unless efforts are made to restore them (Rives *et al.* 1980, Gould *et al.* 1996).

Abiotic properties of the soil amendment may also facilitate successful establishment of native plants by generating an environment that is more conducive for seed germination and recruitment. In our experiment, adding 2 cm of topsoil probably ameliorated the water holding capacity, microclimate, and microtopography compared to bare ash (Chambers *et al.* 1990; Chambers 2000).

Currently over 40 million ha of land are infested with exotic species in North America (Anon. 1998). Our results show that burning slash piles generate scars with increased susceptibility to invasion by exotic plant species. Generally the most opportunistic time to control or reduce non-native species is during early spread before large densities or large areas are occupied (Byers *et al.* 2002). Because of the undesirable long-term effects of slash pile scars, we recommend that land managers minimize burning large piles of slash. If slash pile burning is the only realistic management option for safely reducing large amounts of fuel, then we recommend that slash be piled and burned on dirt roads. We also recommend that severely burned slash pile scars are treated with seed and soil amendments within the first growing season following burning to increase the rate of native plant establishment and discourage the invasion of exotic species. Native seeds of species common in the area should be used from a local source to minimize genetic contamination for seeding amendments, and soil should also be taken from the vicinity.

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LITERATURE CITED

Anon. (1998). Pulling Together: A national strategy for management of invasive plants. 2nd ed. Federal Interagency Committee for Management of Noxious and Exotic Weeds (eds.) (FICMNEW), US Government Printing Office, Washington, DC.

Ballard, T.M. (2000). Impacts of forest management on northern forest soils. *Forest Ecology and Management* 133: 37-42.

Baskin, C.C., & Baskin, J.M. (1998). Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press: San Diego, California.

Berch, S.M., Deom, E., Roth, A. & Beese, W.J. (1993). Vesicular-arbuscular mycorrhizae of western redcedar in container nurseries and on field sites after slash burning. *Tree Planters' Notes* 44: 33-37.

Brundrett, M.C., & Abbott, L.K. (1994). Mycorrhizal fungus propagules in the jarrah forests. I. Seasonal study of inoculum levels. *New Phytologist* **127**:539-546.

Byers, J. E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E. & Hayes, D. (2002).
Directing Research to Reduce the Impacts of Nonindigenous Species. *Conservation Biology* 16: 630-640

Chambers, J.C. (2000). Seed movements and seedling fates in disturbed sagebrush steppe ecosytems: implications for restoration. *Ecological Applications* 10: 1400-1413.

Chambers, J.C., MacMahon, J.A. & Brown, R.W. (1990). Alpine seedling establishment: the influence of disturbance type. *Ecology* 71: 1323-1341.

Covington, W.W., Fulé, P.Z., Moore, M.M., Hart S.C., Kolb, T.E., Mast, J.N., Sackett, S.S. & Wagner, W.R. (1997). Restoring ecosystem health in ponderosa pine forests of the southwest. *Journal of Forestry* 95: 23-29.

Covington, W.W., DeBano L.F., & Huntsberger, T.G. (1991). Soil nitrogen changes associated with slash pile burning in pinyon-juniper woodlands. *Forest Science* 37: 347-355.

Debano, L.F., Rice, R.M., & Conrad, C.E. (1979). Soil heating in chaparral fires: effects on soil properties, plant nutrients, erosion, and runoff. U.S.D.A. Forest Service Research Paper PSW-145.

Dhillion, S.S., Andersen, R.C. & Liberta, A.E. (1988). Effect of fire on the mycorrhizal ecology of little bluestem (*Schizachyrium scoparium*). *Canadian Journal of Botany* 66: 706-713.

Ellingson, L.J., Kauffman, J.B., Cummings, D.L., Sandford Jr., R.L, & Jaramillo, V.J. (2000). Soil N dynamics associated with deforestation, biomass burning, and pasture conversion in a Mexican tropical dry forest. *Forest Ecology and Management* 137: 41-51.

Fuller, W.H., Shannon, S. & Burgess, P.S. (1955). Effects of burning on certain forest soils of northern Arizona. *Forest Science* 1: 44-50.

Gange, A.C., Brown, V.K., & Sinclair, G.S. (1993). Vesicular-arbuscular mycorrhizal fungi: a determinant of plant community structure in early succession. *Functional Ecology* 7: 616-622.

Gange, A.C., Brown, V.K., & Farmer, L.M. (1990). A test of mycorrhizal benefit in an early successional plant community. *New Phytologist* 115: 85-91.

Giovannetti, M., &. Mosse B. (1980). An evaluation of techniques for measuring vesicular-arbuscular mycorrhiza infection in roots. *New Phytologist* 84: 489-500.

Gibson, D.J. & Hetrick, B.A.D. (1988). Topographic and fire effects on the composition and abundance of VA-mycorrhizal fungi on tallgrass prairie. *Mycologia* 80: 433-451.

Gould, A.B., Hendrix, J.W., & Ferriss, R.S. (1996). Relationship of mycorrhizal activity to time following reclamation of surface mine land in western Kentucky. I. Propagule and spore population densities. *Canadian Journal of Botany* 74: 247-261.

Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* 111: 1169-1193.

Hardy, C.C. (1996). Guidelines for estimating volume, biomass, and smoke production for piled slash. U.S.D.A. Forest Service General Technical Report PNW-GTR-364.

Harrington M.G., & Sackett, S.S. (1990). Using fire as a management tool in southwestern ponderosa pine. In: Effects of fire management of southwestern natural resources. USDA Forest Service General Technical Report RM-191, 122-133.

Hartnett, D.C., & Wilson, G.W.T. (1999). Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* 80: 1187-1195.

Hartnett, D.C., Samenus, R.J., Fisher, L.E., & Hetrick, B.A.D. (1994). Plant demographic responses to mycorrhizal symbiosis in tallgrass prairie. *Oecologia* 99: 21-26.

Hassan, M.A., &.West, N.E. (1986). Dynamics of soil seed pools in burned and unburned sagebrush semideserts. *Ecology* 67: 269-272.

Jasper, D.A., Abbott, L.K., & Robson, A.D. (1989). Hyphae of vesicular-arbuscular mycorrhizal fungus maintain infectivity in dry soil, except when the soil is disturbed. *New Phytologist* 112: 101-107.

Jordan, N.R., Zhang, J. & Huerd, S. (2000). Arbuscular-mycorrhizal fungi: potential roles in weed management. *Weed Research* 40: 397-410.

Klemmedson, J.O. (1976). Effect of thinning and slash burning on nitrogen and carbon in ecosystems of your dense ponderosa pine. *Forest Science* 22: 45-53.

Klironomos, J. N. (2002). Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417: 67-70.

Klopatek, C.C., Debano, L.F., & Klopatek, J.M. (1988). Effects of simulated fire on vesicular-arbuscular mycorrhizae in pinyon-juniper woodland soil. *Plant and Soil* 109: 245-249.

Korb, J.E., Johnson, N.C., & Covington, W.W. (2001). Preliminary results-The effects of restoration thinning on mycorrhizal fungal propagules in a northern Arizona ponderosa pine forest. In: Vance, G.K., Covington, W. W., & Edminster, C.E. (compilers), Ponderosa Pine Ecosystems Restoration and Conservation: Steps Toward Stewardship. Proc. RMRS-P-22. Ogden, Utah. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Koske, R.E., & Gemma, J.N. (1990). VA mycorrhizae in strand vegetation of Hawaii: evidence for long-distance codispersal of plants and fungi. *American Journal of Botany* 77: 466-474.

Moore, J.M., & Wein, R.W. (1977). Viable seed populations by soil depth and potential site recolonization after disturbance. *Canadian Journal of Botany* 55: 2408-2412.

Moreno, J.M., & Oechel, W.C. (1991). Fire intensity effects on germination of shrubs and herbs in southern California chaparrel. *Ecology* 72: 1993-2004.

Neary, D.G., Klopatek, C.C., DeBano, L.F., & Ffolliott, P.F. (1999). Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* 122: 51-71.

Odion, D.C., & Davis, F.W. (2000). Fire, soil heating, and the formation of vegetation patterns in chaparral. *Ecological Monographs* 70: 149-169.

Parkinson, J.A., & Allen, S.E. (1975). A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. *Cummun. Soil Science and Plant Analysis* 6: 1-11.

Pattinson, G.S., Hammill, K.A., Sutton, B.G., & Mcgee, P.A. (1999). Simulated fire reduces the density of arbuscular mycorrhizal fungi at the soil surface. *Mycological Research* 103: 491-496.

Pratt, D.W., Black, R.A., & Zamora, B.A. (1984). Buried viable seed in a ponderosa pine community. *Canadian Journal of Botany* 62: 44-52.

Rashid, A., Ahmed T., Ayub, N., & Khan, A.G. (1997). Effect of forest fire on number, viability and post-fire re-establishment of arbuscular mycorrhizae. *Mycorrhiza* 7: 217-220.

Rives, C.S., Bajwa, M.I., Leberta, A.E., & Miller, R.M. (1980). Effects of topsoil storage during surface mining on the viability of VA mycorrhizae. *Soil Science 129*: 253-257.

Roberts, W.B. (1965). Soil temperatures under a pile of burning logs. *Australian Journal of Forest Research* 1: 21-25.

Rundel, P.W. (1983). Impact of fire on nutrient cycles in Mediterranean-type ecosystems with reference to chaparral. In: Kruger, F.J., Mitchell, D.T., Jarvis, J. U.M. eds. Mediterranean-Type Ecosystems: The Role of Nutrients. Springer-Verlag, New York, New York, USA, 192-207.

Schenck, N.C., Graham, S.O., & Green, N.E. (1975). Temperature and light effect on contamination and spore germination of VA mycorrhizal fungi. *Mycologia* 67: 1189-1192.

Shubert G.H. (1974). Silviculture of southwestern ponderosa pine: the status of our knowledge. USDA Forest Service Research Paper RM-123.

Smith, M.R., Charvat, I., & Jacobson, R.L. (1998). Arbuscular mycorrhizae promote establishment of prairie species in a tallgrass prairie restoration. *Canadian Journal of Botany* 76: 1947-1954.

Smith, S.E., & Walker, N.A. (1981). A quantitative study of mycorrhizal infection in Trifolium: separate determination of the rates of infection and of mycelial growth. *New Phytologist* 89: 225-240.

St. John, T.V., Coleman, D.C., & Reid, C.P.P. (1983). Association of vesicular-arbuscular mycorrhizal hyphae with soil organic particles. *Ecology* 64: 957-959.

Terrestrial Ecosystems Survey of the Coconino National Forests. 1995. U.S. Department of Agriculture, Forest Service, Southwest Region.

Van der Heijden, M., Klironomos, J. N., Ursic, M., Moutoglis, P., Streitwolf-Engle, R., Boller, T., Wiemken, A., & Sanders, I. R. (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature* 396: 69-72.

Weast, R.C. (1988). Handbook of Chemistry and Physics. CRC Press: Boca Raton, Florida.

Zar, J. H. (1984). Biostatistical analysis, 2nd ed. Prentice-Hall. Englewood Cliffs, New Jersey, USA.

Table 1. Seeded species' average cover for the seed and seed/soil amendment plots in 2000 and 2001. Data are expressed as means (N=30) ± SE.

Species	Average Cover (2000)		Average Cover (2001)	
	Seed	Seed/Soil	Seed	Seed/Soil
Grasses				
Bouteloua gracilis	0.03 ±.01a	0.35 ±.06b	0.07 ±.03a	0.26 ±.06b
Elymus elymoides	0.10 ±.03a	0.41 ±.07a	2.02 ±.96a	6.12 ±1.3b
Festuca arizonica	0.01 ±.01a	0.02 ±.01a	0.07 ±.03a	0.14 ±.07a
Koeleria macrantha	*	*	*	*
Muhlenbergia wrightii	0.02 ±.02a	0.13 ±.02b	0.17 ±.09a	0.82 ±.30b
Poa fendleriana	*	*	*	*
Schizachyrium scoparium	*	*	*	*
Forbs				
Artemisia ludoviciana	0 ± 0a	0.06 ±.04a	0.02 ±.01a	0.14 ±.04b
Castilleja linariifolia	*	*	*	*
Geum triflorum	*	*	*	*
Heliomeris multiflora	0.01 ±.01a	0.04 ±.02a	0.48 ±.21a	0.36±.13a
Ipomopsis aggregata	0.02 ±.01a	0.12 ±.02b	1.07 ±.25a	2.16 ±.49b
Iris missouriensis	0 ±.0a	0 ± 0a	0 ± 0a	0.01 ±.01a
Linum lewisii	0.01 ±.01a	0.11 ±.04b	0 ± 0a	0.13 ±.07b
Lupinus argenteus	0.02 ±.01a	0.01 ±.01a	0.02 ±.01a	0.01 ±.01a
Oxytropis lambertii	0.03 ±.01a	0.06 ±.02a	0.22 ±.21a	0.28 ±.22a
Penstemon barbatus	0 ± 0a	0 ± 0a	0.51 ±.21a	0.59 ±.13a
Penstemon virgatus	0 ± 0a	0 ± 0a	0.02 ±.01a	0.18 ±.08b
Thermopsis divaricarpa	0 ± 0a	0 ± 0a	0 ±.01a	0.12 ±.02b

* Species that did not germinate or did not establish as seedlings during the 2000 or 2001 growing season.

FIGURE HEADINGS

Figure 1. The relative amount of mycorrhizal propagules indicated by percent AM colonized root length in corn from bait-plant bioassays along the fire intensity gradient in 2000 and 2001, 7 months and 19 months following burning. Differences between the locations along the fire intensity gradient were determined by MANOVA repeated measures on arcsin square root transformed data. Values indexed by different letters are significantly different at the $p \leq 0.05$ level.

Figure 2. The density of viable seeds of native, ruderal, and exotic plant species along the slash pile gradient in 2000, 7 months after burning. Differences between the locations along the gradient were determined by ANOVA on log(x+1) transformed data. Values indexed by different letters are significantly different at the $p \leq 0.05$ level.

Figure 3a-c. Soil chemical properties along the fire intensity gradient for 2000, 7 months after burning. Differences between the locations along the fire intensity gradient were determined by ANOVA on square-root transformed data. Values indexed by different letters are significantly different at the $p \leq 0.05$ level.

Figure 4. Relative root colonization with AM fungal structures (arbuscules, vesicles, hyphae) in corn roots grown in soils collected in 2001 from the control plots and plots amended with sterilized soil (no propagules), and both seed and live soil. Differences between the AM fungal structures were determined by ANOVA on arcsin square root transformed data. Values indexed by different letters are significantly different at the $p \leq 0.05$ level.

Figure 5a-d. Average cover of a). forbs, b). graminoids, c). exotic plants, and d). ruderal species established under different amelioration treatments. Differences between treatments were determined by MANOVA repeated measures. The symbol * indicates that herbaceous plant cover was zero.

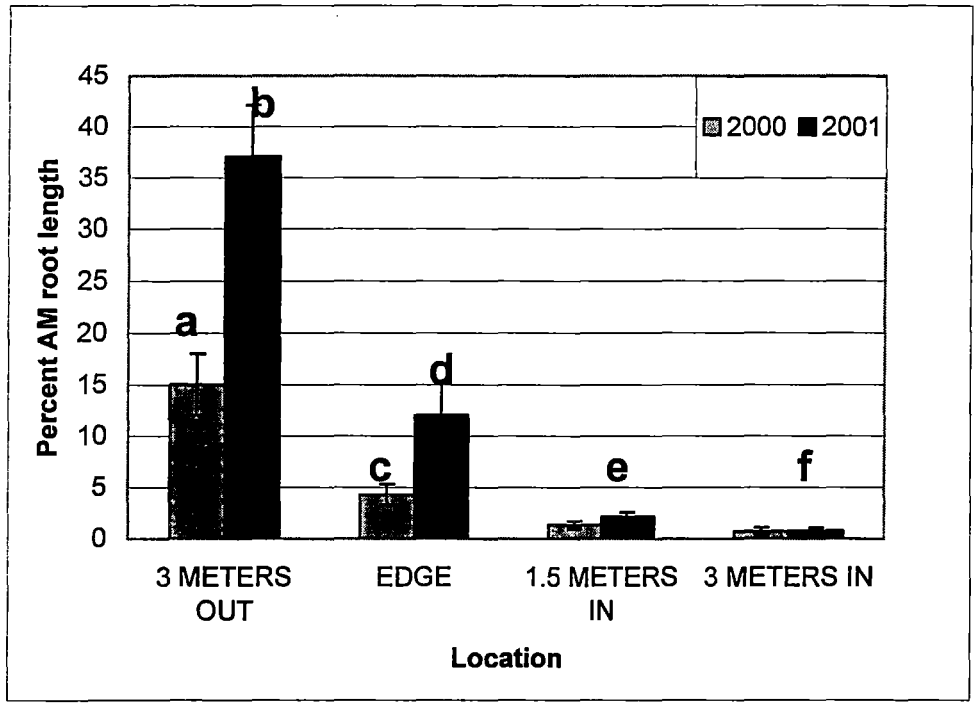

45
40
35
30
25
20
15
10
5
0
Percent AM root length
2000
2001
a
b
c
d
e
f
3 METERS OUT
EDGE
1.5 METERS IN
3 METERS IN
Location

Figure 1.

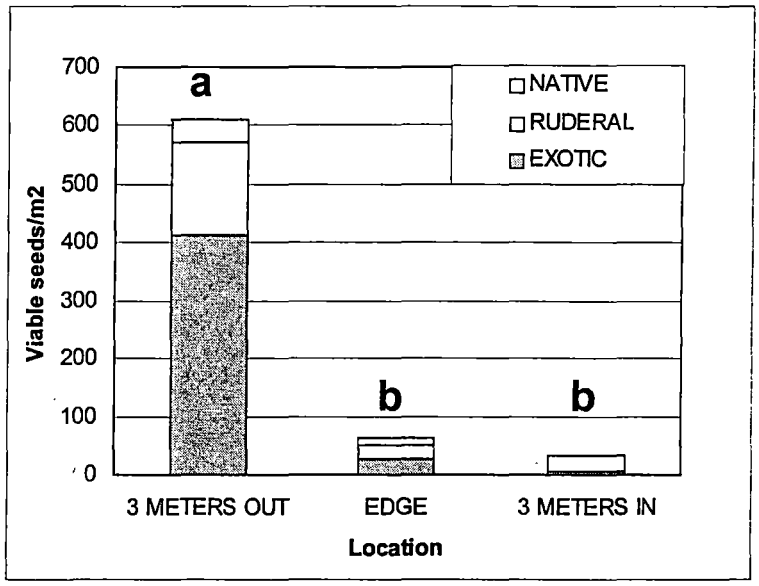

700
600
500
400
300
200
100
0
Viable seeds/m2
a
b
b
NATIVE
RUDERAL
EXOTIC
3 METERS OUT
EDGE
3 METERS IN
Location

Figure 2.

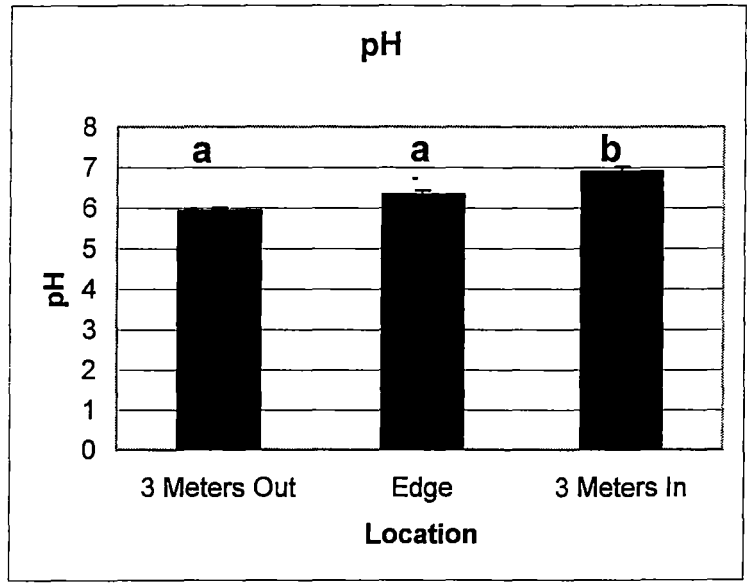


Figure 3a.

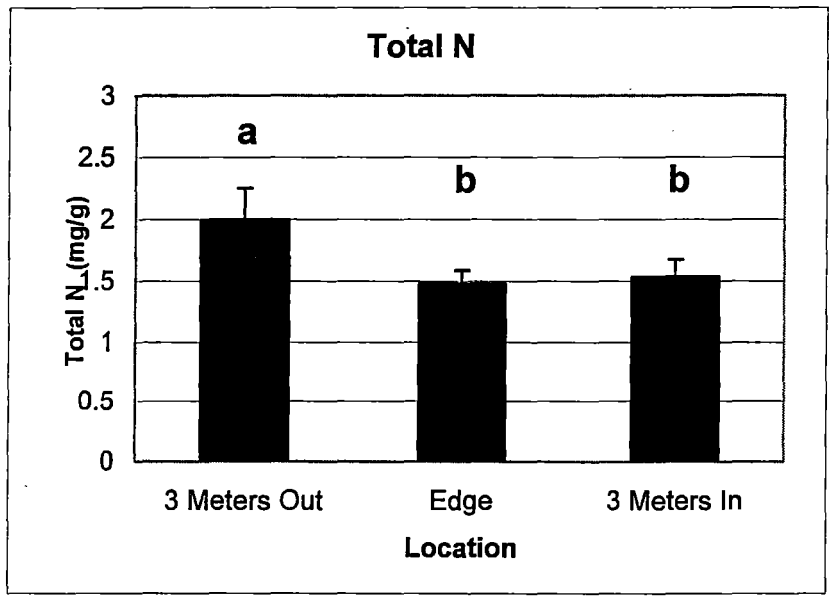


Figure 3b.

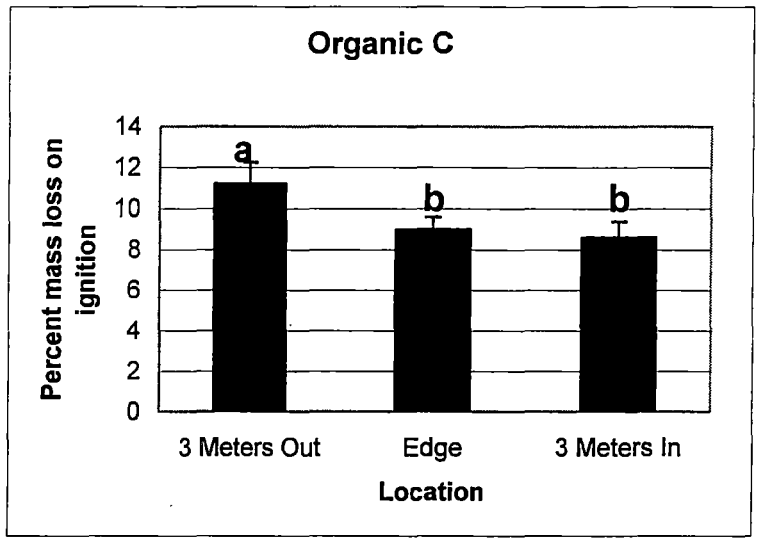


Figure 3c.

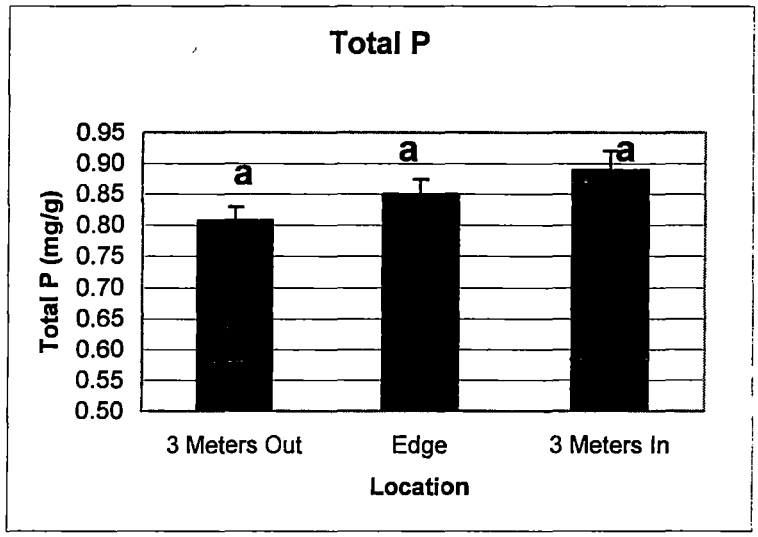


Figure 3d.

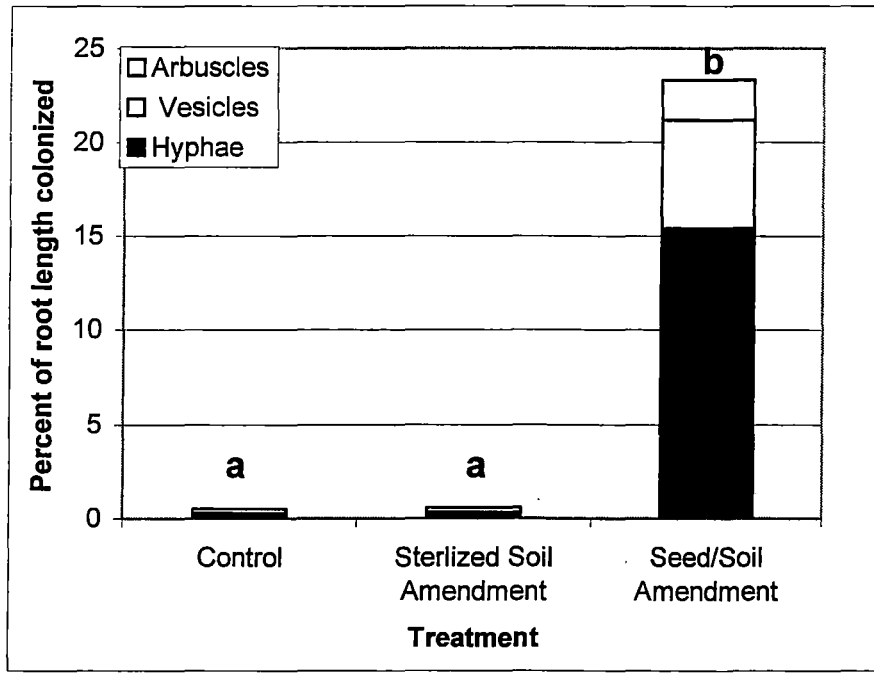

Percent of root length colonized
25
20
15
10
5
0
Arbuscles
Vesicles
Hyphae
a
a
b
Control
Sterlized Soil Amendment
Seed/Soil Amendment
Treatment

Figure 4.

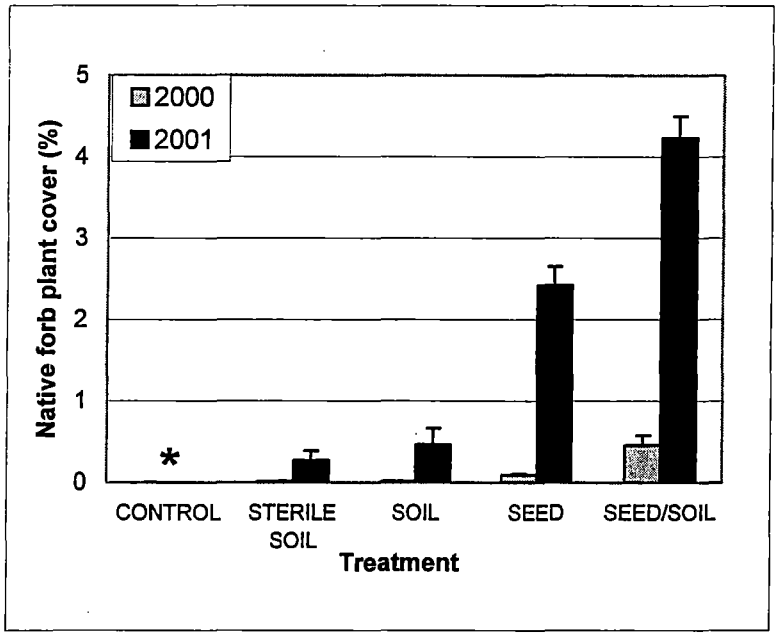


Figure 5a.

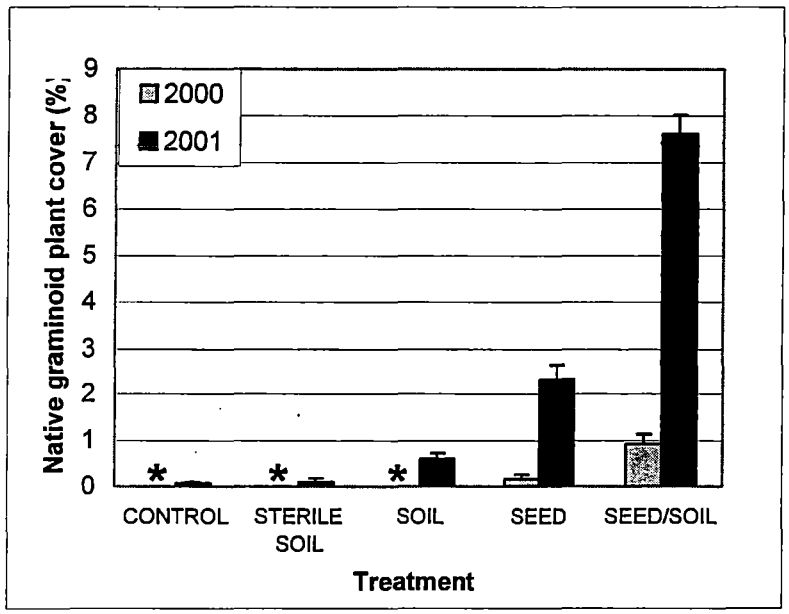


Figure 5b.

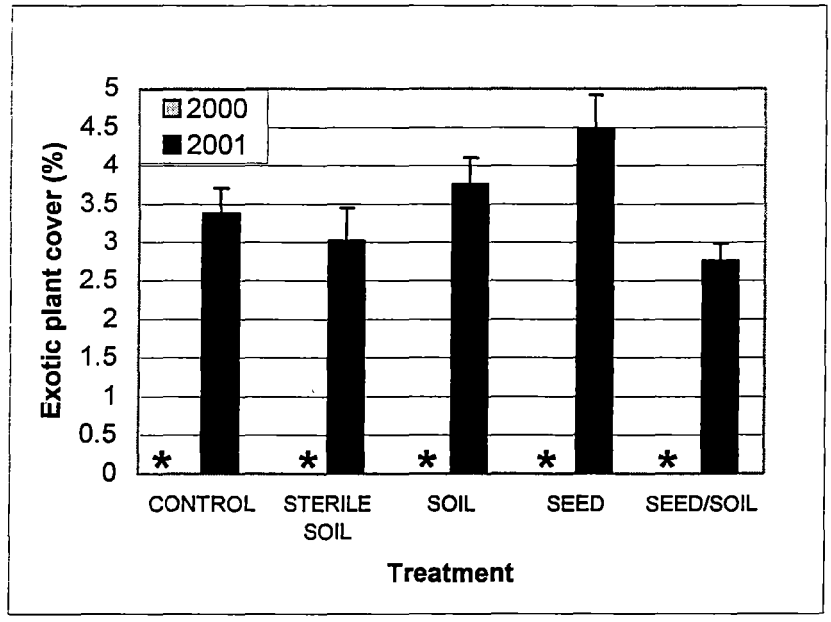


Figure 5c.

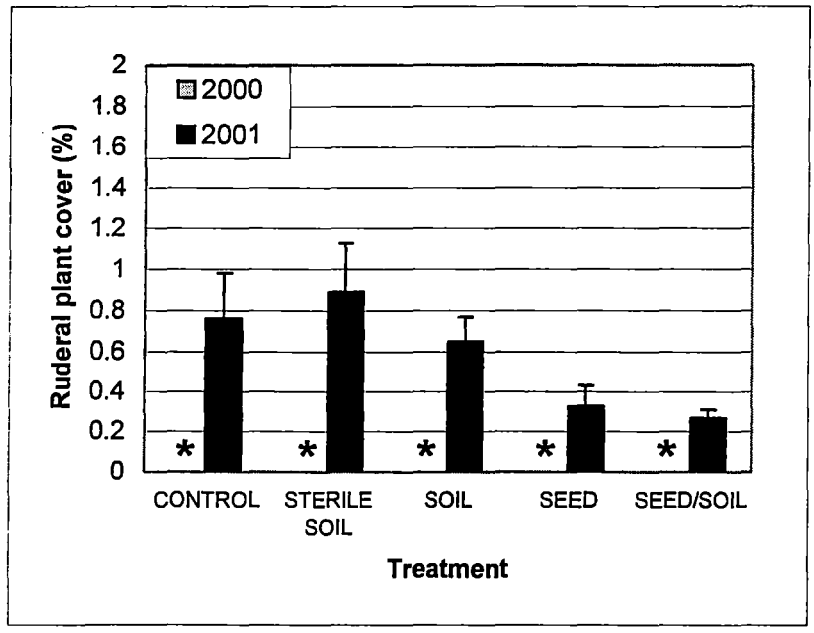


Figure 5d.

Soil Disturbance and Herbaceous Response Associated with Different Harvest Systems and Intensities

Abstract

Tree thinning is often associated with changes in soil processes and herbaceous composition and productivity. This study was conducted to quantify the effect of different harvest systems and thinning intensities on forest floor disturbance and short-term herbaceous vegetation responses in ponderosa pine forest restoration in northern Arizona. Tree thinning intensity did not significantly affect soil disturbance, dead woody biomass or herbaceous vegetation response. In contrast, the whole-tree harvest system had the largest proportion of high soil disturbance (13%) and the lowest dead woody biomass (38.9 Mg/ha) compared to the machine and hand harvest systems. The whole-tree system had a significant increase (14%) in the proportion of non-native herbaceous cover three years following the initial treatments, which was associated with soil profile disturbance and previous management history; there were no significant differences for the machine or hand systems. These results suggest that the harvest system has a greater impact on forest soils and herbaceous vegetation than the intensity of tree removal and that the response of the herbaceous vegetation to tree thinning is a complex interaction of numerous ecological variables related to previous and current forest management.

Introduction

Different harvest systems (types of equipment) and thinning intensities (number of tree removal) are being used in ponderosa pine restoration to cut and extract large numbers of small diameter trees. Many southwestern ponderosa pine (Pinus ponderosa Dougl. ex Laws.) forests currently consist of numerous small trees, with high fuel loads and low herbaceous understory diversity and productivity, as the result of heavy livestock grazing, intensive logging of old-growth trees, and fire suppression following Euro-American settlement in the mid 1880's (Covington et al. 1994). Ponderosa pine restoration aims to restore ecosystem structure and function within a range of natural variability primarily through tree thinning and prescribed fire (Moore et al. 1999, Lynch et al. 2000). Tree thinning can significantly affect soil processes and tree and herbaceous productivity due to soil profile disturbance and compaction (Jurgensen et al. 1997, McNabb et al. 2001). In addition, soil disturbance intensity has been associated with increased abundance of non-native and early successional native species following disturbance (Kotanen 1997, Stylinski and Allen 1999), so restoration thinning treatments that cause high soil disturbance may delay the positive effects of restoration treatments on the herbaceous understory community. The amount of soil disturbance associated with tree thinning often varies with the type of equipment used, the amount of tree removal, the timing of thinning (e.g., soil moisture content), and the soil type (e.g., amount of soil surface organic matter) (Greacen and Sands 1980, Howard et al. 1981, Rab 1996).

Currently extensive thinning is being advocated in northern Arizona to reduce unnatural high tree densities. Conducting large-scale studies to measure differences in thinning intensities and harvest systems is difficult because of the logistics and expense of moving equipment considerable distances to treat different areas. The primary focus of this study was to determine if different thinning intensities had different effects on

ecological variables and the response of ecological variables to different harvest systems was secondary. In our study, we randomly located different thinning intensities within individual experimental blocks; we were not able to randomly located different harvest systems in each block. As a result, because a particular harvest system was only applied within one block our inferences are limited. However, the inferences that we can make still contribute to the overall understanding of how different harvest systems affect different ecological variables.

The specific objectives of this study were to: 1) determine the level of soil disturbance by categorizing soil profile disturbance in experimental areas thinned using different intensities and harvest systems; 2) determine the effect of different thinning intensities and harvest systems on soil bulk density and dead woody biomass; and 3) determine the effect of different thinning intensities and harvest systems on short-term herbaceous vegetation responses (native versus non-native). We hypothesized that the intensity of thinning would not significantly affect soil disturbance, because current literature shows that the majority of soil profile disturbance and compaction is created during the initial passes of thinning equipment (Gent et al. 1984, Rab 1996). We also hypothesized that different harvest systems would have varying effects on soil disturbance, based upon studies that illustrated significantly greater soil profile disturbance and compaction in areas that were thinned creating skid trails than areas without skid trails (Dickerson 1976, Incerti et al. 1987) and that areas with greater soil disturbance would have higher proportions of non-native species.

Methods

Study Site

The study was conducted within an approximately 688 ha area of the Fort Valley Experimental Forest and adjacent Coconino National Forest approximately 16 km northwest of Flagstaff, Arizona. The vegetation at the study site consisted of pure ponderosa pine stands, with few large trees intermixed with numerous small trees. Dominant grass species include mountain muhley (Muhlenbergia montana), Arizona fescue (Festuca arizonica) and muttongrass (Poa fendleriana). The elevation is ~2230 m with an average of 94 frost-free growing days. Average summer precipitation is 20.83 cm in the Flagstaff area (NOAA). Precipitation patterns include scattered snowfall and rain during the winter months, a pronounced drought in May and June, followed by frequent monsoon rains in July and August.

Experimental Design

The Forest Service and Grand Canyon Forests Partnership established three blocks of four different treatments during the summer of 1998 (Figure 1). Each treatment unit was approximately 16 hectares. Treatment units within each block were randomly assigned one of four treatments: (1) no thinning or burning (control); (2) thinning to a high level of remaining trees (low intensity); (3) thinning to an intermediate level of remaining trees (intermediate intensity); and (4) thinning to a low level of remaining trees more similar to the forest density prior to European settlement circa 1876 (high intensity). A tree needed to be taller than breast height (1.37 m) to be counted. All thinned treatment units were treated with prescribed fire.

For all thinning treatments, the reference condition was the pre-settlement pattern of tree species composition and spatial arrangement (Fulé et al. 2001). All living pre-

settlement trees of all species were retained for all thinning treatments. In addition, wherever we encountered remnant pre-settlement material (snags, stumps, logs), several of the largest post-settlement trees of the same species within 9.1 m were retained as replacements. If no suitable trees were located within 9.1 m, the search radius was extended to 18.2 m. For the high intensity treatment, each remnant was replaced with 1.5 trees (i.e. three replacements per two remnants) if the replacements were 40.6 cm diameter at breast height (dbh) or larger, or 3 trees if the replacements were <40.6 dbh. In the intermediate intensity treatment, each remnant was replaced with 2 trees if the replacements were >40.6 cm dbh or larger or 4 trees if the replacements were <40.6 dbh. For the low intensity treatment, 3 trees were used as replacements for each remnant if the replacements were >40.6 cm dbh or larger or 6 six trees if the replacements were <40.6 dbh (see Fulé et al. 2001 for detailed description of thinning design).

Each block was treated using different harvest systems. All harvest systems were implemented during dry weather conditions. Block 1 (machine) was logged between fall 1998 and 1999 using a cut-to-length head on a small excavator. Yarding was done with a rubber tired forwarder and logs were directly placed on haul trucks. Block 1 was prescribed burned in spring 2001. Fellers with chain saws logged Block 2 (hand) between fall 1998 and 1999. Yarding was done with a rubber tired forwarder to landings. In fall 2000, a small dozer was used to pile slash to reduce fire hazard and to permit broadcast prescribed burning. Slash piles were burned in winter 2001 and the area was prescribed burned in spring 2001. Block 3 (whole-tree) was logged between fall 1998 and winter 1999 (March) when the soils were dry or frozen. A feller-buncher was used to harvest trees and yarding was done with a rubber tired skidder. A de-limber/bucker was used at landing areas where decks and slash piles were created. Slash piles were burned in the winter of 2000 and the area was prescribed burned in spring 2000.

Soils

Soils are moderately well-drained clays and clay loams derived from flow and cinder basalt. The A horizon extends only to 10 cm, with the remaining soil profile reaching between 114 to 152 cm depth before reaching the fractured basalt bedrock (Overby, 2002, personal communication). All three experimental blocks included two classified soils: (1) a loamy-skeletal, mixed Mollic Eutroboralf (Block 1 low intensity, Block 2 low intensity, and Block 3 control) and (2) a fine, montmorillonitic Mollic Eutroboralf (Block 1 and Block 2 intermediate and high intensity and control, and Block 3 low intensity). The soils found in Block 3's intermediate and high intensity thinning treatments are classified as fine, montmorillonitic Typic Argiboroll (Terrestrial Ecosystem Survey of the Coconino National Forest, TES 1995). The fine, montmorillonitic Mollic Eutroboralf and fine, montmorillonitic Typic Argiboroll soils were both classified as being subject to soil damage (compaction and displacement) when wet; problems could be mitigated if ground disturbing activities were limited to periods when the soils were dry (TES 1995).

Field Sampling

Sampling was conducted on twenty permanently located plots on a 60 m grid within each treatment unit. Overstory trees taller than breast height (1.37 m) were measured on a 400 m^2 circular fixed-area plot in 1998 and 2000. Every year between 1998 and 2001 we recorded plant species, forest floor substrate, and overstory canopy cover (vertical projection) every 30 cm along a 50 m line transect. In addition, dead

woody biomass and forest floor depth were measured along the same 50 m transect following thinning in 1999 following the method of Brown (1974).

Soil profile disturbance was visually assessed and categorized into five different groups in 1999 along the entire 50 m line transect based upon a soil profile disturbance classification similar to the method established by Rab (1994). The five disturbance groups included: (1) bladed road, (2) heavy disturbance, (3) intermediate disturbance, (4) light disturbance, and (5) no disturbance (Figure 2a). A bladed road is any area where a road was constructed to remove timber. Heavy disturbance is any area where more than 75% of the O-horizon has been removed or disturbed and/or where deep gouges or ruts are visible in the mineral soil (Figure 2b). Moderate disturbance is any area where 40-75% of the O-horizon has been removed or disturbed due to harvesting activity. Light disturbance is any area where less than 40% of the O-horizon has been removed due to harvesting activity. Bulk density was sampled at 20 m along each transect in 1999 to quantify soil compaction (n=20/unit). A cylindrical metal bulk density sampler 4.8 cm diameter was taken to a depth of 10 cm, 0.5 m away from the transect to prevent disturbance on the transect. Soil samples were oven-dried for 24 hr at 105° C to determine bulk density (Page-Dumroese et al. 1999). Bulk density was not corrected for rock fragments because few samples had fragments. Samples that had rock fragments were minimal in content, or occasionally, their presence prevented the collection of an undisturbed core when pushing the ring into the ground (McNabb et al. 2001). Total bulk density was determined by dividing the oven-dry mass by sample volume.

Statistical Analysis

We used analysis of variance (ANOVA) to determine the effect of thinning on soil disturbance and bulk density for data collected in 1999. We used repeated measures multivariate analysis of variance (MANOVA) in SPSS version 8 (SAS Institute 1997) to determine the effect of thinning on trees/hectare, tree basal area, tree canopy and non-native species abundance, and the effect of slash piling on soil disturbance following initial thinning treatments using the hand technique. The Shapiro Wilk test was used to test data for normality, and Leven's test was used to test for homogeneity of the variance (Milliken and Johnson 1984). Prior to analysis, data were square root transformed as necessary to improve normality and homoscedasticity assumptions (Zar 1984). Tukey's Honestly Significant Difference (HSD) test was used to make multiple comparisons of means following a significant result. PC-ORD software was used to determine variation in herbaceous community richness and abundance between native and non-native species using non-metric multidimensional scaling (NMDS), multi-response permutation procedures (MRPP), and indicator species analysis (McCune and Mefford 1999).

Results

Soil Disturbance

Intensity of thinning did not cause significant differences in soil profile disturbance (Figure 3a), soil bulk density (Table 1) or dead woody biomass and forest floor depth (Table 2). In contrast, different harvest systems did have significant differences in soil profile disturbance and dead woody biomass (Figure 3b); but there were no significant differences in soil bulk density (Table 1) or forest floor depth (Table 2). Specifically, there was a significantly lower proportion of the study area that had no disturbance that was thinned using the whole-tree system (41.3 %) than by machine (64.5

%) or hand (64.9 %) (Figure 3b). In contrast, there was a significantly higher proportion of the study area that had high disturbance that was thinned using the whole-tree system (13 %) than by machine (3 %) or hand (2.3) (Figure 3b). Intermediate disturbance with the whole-tree system (22.3%) was almost double that done by the machine system (10 %) or hand system (11.3 %); however, these differences were not significant (Figure 3b). Total woody debris was significantly lower in areas treated with the whole-tree system (38.94 kg/ha) than the machine system (63.16 kg/ha) or hand system (66.69 kg/ha) (Table 3). In Block 2 (hand) where soil profile disturbance was measured before and after slash piling, there was a significantly larger area that had no disturbance prior to piling (64.9 %) than after piling (29.2 %) (Figure 3c). In addition, there was significantly lower high disturbance prior to piling (2.3 %) than after piling (14.2 %) (Figure 3c).

For all thinning intensities and harvest systems, trees/hectare, tree basal area, and tree canopy cover declined significantly from pre-treatment to post-treatment (Table 3). There was no significant difference between pre-treatment and post-treatment trees/hectare, tree basal area, and tree canopy cover in the controls (no thinning/burning) (Table 3). In addition, there was no significant difference among post-treatment trees/hectare, tree basal area, and tree canopy cover among different thinning intensities or among different harvest systems due to high variances (Table 3).

Herbaceous Vegetation Response

There was a significant increase in the proportion of non-native cover between pretreatment and post-treatment for the whole-tree system (Table 4). There was no significant difference in the proportion of non-native cover for either the machine or hand systems or any of the different thinning intensities (Table 4). Herbaceous community analysis using NMDS showed there was no significant difference between thinning intensities across time (Figure 4a) and indicator species analysis showed no indicator species (data not shown). In contrast, NMDS showed significant differences between the post-treatment (2001) herbaceous communities thinned with different harvesting systems (Figure 4b). Vector analysis showed that these differences were associated with the proportion of native or non-native species and the intensity of soil disturbance (Figure 4b). Specifically, wooly mullein (Verbascum thapsus) (0.003), pineland marshtail (Laennecia schiedeana) (0.004), Navajo cinquefoil (Potentilla subviscosa) (0.01) and Dalmation toadflax (Linaria dalmatica) (0.049) all had significant indicator values as determined by indicator species analysis.

Discussion

Soil Disturbance

Ecological restoration was defined by the Society of Ecological Restoration (1997) as "the process of assisting the recovery and management of ecological integrity. Ecological integrity includes a critical range of variability in biodiversity, ecological processes and structures, regional and historical context, and sustainable cultural practices." While reducing tree density and prescribed burning are two necessary components to restore southwestern ponderosa pine ecosystems (Covington et al. 1997, Lynch et al. 2000), restoration thinning and prescribed burning treatments should be designed to minimize their impact on the ecological integrity of the ecosystem. Soils are important to the ecological integrity of an ecosystem, playing a role in ecosystem function and vegetation responses following disturbance (Wali 1999). For example, a

study conducted at our same research site showed that burning large piles of tree slash altered soil physical and chemical properties, significantly reduced arbuscular mycorrhizal (AM) propagule densities, viable seeds in the soil seed bank, extant vegetation, and increased the susceptibility to exotic species invasion (Korb et al. in review), illustrating how severe disturbances can have adverse affects on ecological integrity and achieving restoration goals.

Some have suggested that multiple staged thinning entries should be conducted instead of one thinning entry that removes large numbers of trees at one point in time to reduce the initial disturbance intensity due to the removal of large tree numbers (Allen et al. in press). Our study results do not suggest that multiple staged thinning entries will reduce initial soil disturbance. Thinning intensity (whether you remove a small number of trees or large number of trees) did not have a significant effect on soil disturbance; therefore, removing a larger number of trees at one thinning entry does not necessarily result in higher soil disturbance. These results are consistent with other soil disturbance studies that illustrate soil disturbance and compaction generally occur during the first few entries of mechanized equipment (Gent et al. 1984, McNabb et al. 2001). In contrast, we found that the harvesting system used to remove trees did have a significant effect on soil disturbance and herbaceous plant recovery. Specifically, our study showed logging using a cut-to-length head on a small excavator (machine) and felling with chain saws and yarding with a rubber tired forwarder to landings (hand) resulted in significantly less soil profile disturbance than using a feller-buncher and yarding with a rubber tired skidder (whole-tree). While this component of our study design has some limitations because the harvest systems was the same for each block, our data are consistent with numerous other studies that have shown tree-length harvesting with a rubber tired skidder causes soil disturbance and compaction (Dickerson 1976, Jakobensen and Moore 1981, Rab 1996, Brais 2001). In addition, when the number of trees removed during harvesting is compared among blocks, Block 3 had the lowest number of trees removed in comparison to Block 1 or 2 (Table 2). So even while there were fewer trees being removed from Block 3 for all the different thinning intensities, Block 3 still had significantly higher soil profile disturbance than the other blocks.

Contrary to expectations, our study did not show significant changes in soil compaction. We sampled for soil compaction on systematically located transects throughout the entire study unit so we most likely missed the areas that were compacted due to skidding. Other soil disturbance studies have shown that generally there are only significant changes in soil compaction in small portions of the harvested area and that locating sampling areas in skid trails and landing areas using stratified sampling is necessary to accurately quantify soil compaction associated with skid trails and landing areas (Incerti et al. 1987, Rab 1996). As a result, we recommend that future studies use a stratified random sampling approach to quantify soil disturbance in severely disturbed areas such as skid trails and landing areas. In addition, while we only sampled for changes in soil compaction, other soil physical properties may have been altered due to disturbance, including decreased macroporosity, redistribution of organic matter, decreased infiltration rates, and increased surface runoff (Rab 1994). These are all properties that should be quantified to provide a more comprehensive understanding of how soil disturbance affects ecosystem function.

Herbaceous Vegetation Response

An empirical biological rule is that invasions are frequently associated with disturbance (Kotanen 1997). Available propagule abundance may set limits on the herbaceous community revegetation potential (Kotanen 1997) and the disturbance (size, severity, and timing) may determine the seedling environment and what species are able to establish (Chambers et al. 1990). Non-native species cover only increased significantly following thinning using a feller-buncher and yarding with a rubber tired skidder (whole-tree), which was also the harvesting system associated with the highest soil profile disturbance. However, the whole-tree system harvest area had significantly higher non-native and ruderals viable seeds in the soil seed bank than the areas treated with the machine and hand systems (Korb, unpublished data). The control for the whole-tree system also had a similar amount of non-native and ruderal viable seeds but did not have associated increases in non-native and ruderal species in the extant vegetation over the same time period indicating that something associated with the harvest system, most likely soil disturbance, allowed these species to become established in the areas thinned using the whole-tree system.

Other studies have illustrated a correlation between severe soil disturbance and high non-native vegetation cover (Kotanen 1997, Stylinski and Allen 1999). Ordination of the herbaceous plant communities showed that there were significant differences between the plant communities before and after thinning and among different harvesting systems. Two of the four indicator species were non-native and one was a ruderal (species that prefers high-nutrient disturbed habitats). Vector analysis showed there was a significant relationship between the proportion of non-native species abundance and the amount of soil disturbance. The angle and the length of these vectors indicated that there was a strong relationship between soil disturbance, non-native species cover, and the post-treatment plant communities that were thinned using the whole-tree system as well as some of the other harvest systems. This indicates that while the whole-tree system did result in high soil profile disturbance and high non-native species abundance, there are other factors besides soil disturbance (e.g., the soil seed bank) that facilitated the establishment of non-native species since non-natives were also present in some of the other areas treated with different harvest systems.

Conclusions

Increased soil disturbance from tree thinning is often associated with increased harvesting mechanization and the use of larger machines (Malmer and Grip 1990, McNabb et al. 2001). Soil disturbance, however, is the result of numerous interacting factors such as the amount of tree removal, the timing of thinning (e.g, soil moisture content), and the soil type (e.g. amount of soil surface organic matter) and not simply the type of equipment used. Our study results suggest that thinning with a feller buncher (machine) and yarding with a rubber tired skidder (whole-tree) causes higher soil profile disturbance than the other harvesting systems used in this study. Because we were not able to implement different harvesting systems in different blocks our inferences are limited. We believe however that the differences in soil disturbance among harvest systems was influenced by the type of the equipment use because other factors were either similar among blocks or where differences occurred we found contradictory results ((e.g., areas with higher tree removal, Blocks 1 and 2, did not have more soil profile

disturbance than Block 3 (Figure 3)).

From the findings in this study, we recommend that land managers choosing a harvesting system for restoration should try to design treatments that will minimize unnecessary disturbance. Specifically, managers should choose the harvesting system on a site-specific basis taking into account ecological components (e.g., soil type, soil texture, soil bulk density, soil moisture content at time of thinning), economic constraints (e.g., amount of money and time available to remove trees), and feasibility (e.g., type of mechanized equipment available). By including ecological components, which are not always included in the process of choosing harvesting systems, the outcome of the thinning treatment will be more compatible with restoration goals.

References

Allen, C.D., M. Savage, D.A. Falk, K.F. Suckling, T.W. Swetnam, T. Schulke, P.B. Stacey, P. Morgan, M. Hoffman, and J.T. Klingel, in press. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecological Applications.

Brais S. 2001. Persistence of soil compaction and effects on seedling growth in northwestern Quebec. Soil Science Society of America Journal 65: 1263-1271.

Brown, J. K. 1974. Handbook for inventorying downed woody material. United States Department of Agriculture Forest Service General Technical Report INT-16, Intermountain Forest and Range Experiment Station, Ogden, UT.

Chambers, J.C., J.A. MacMahon, and R.W. Brown. 1990. Alpine seedling establishment: the influence of disturbance type. Ecology 71: 1323-1341.

Covington, W.W., P.Z. Fulé, M.M. Moore, S.C. Hart, T.E. Kolb, J.N. Mast, S.S. Sackett, and W.R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. Journal of Forestry 95: 23-29.

Covington, W.W., R.L. Everett, R.W. Steele, L.I. Irwin, T.A. Daer, and A.N.D. Auclair. 1994. Historical and anticipated changes in forest ecosystems of the Inland West of the United States. Journal of Sustainable Forestry 2: 13-63.

Dickerson, B.P. 1976. Soil compaction after tree-length skidding in northern Mississippi. Soil Science Society of America Journal 40: 965-966.

Fulé, P.Z., C. McHugh, T.A. Heinlein, and W.W. Covington. 2001. Potential fire behavior is reduced following forest restoration treatments. In: Vance, G.K., W.W. Covington, C.B. Edminster (Eds.),Ponderosa Pine Ecosystems Restoration and Conservation: Steps Toward Stewardship Proceeding. Ogden, Utah. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, RMRS-P-22, 28-35.

Howard, R.F., M.J. Singer, and G.A. Frantz. 1981. Effects of soil physical properties, water content, and compactive effort on the compaction of selected California forest and range soils. Soil Science Society of America Journal 45: 231-236.

Gent, J.A. Jr., R. Ballard, A.E. Hassan, and D.K. Cassel. 1984. Impact of harvesting and site preparation on physical properties of piedmont forest soils. Soil Science Society of America Journal 48:173-177.

Greacen, E.L. and R. Sands. 1980. A review of compaction of forest soils. Australian Journal of Soil Research 18: 163-189.

Jakobsen, B.F. and G.A. Moore. 1981. Effects of two types of skidders and of a slash

cover on soil compaction by logging of mountain ash. Australian Forest Research 11: 247-255.
Jurgensen, M.F., A.E. Harvey, R.T. Graham, D.S. Page-Dumroese, J.R. Tonn, M.J. Larsen, and T.B. Jain. 1997. Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of inland northwest forests. Forest Science 43: 234-241.
Korb, J.E., W.W. Covington, and N.C. Johnson. Soil biotic and abiotic changes following slash pile burning and amendments to ameliorate these changes on native plant establishment. Ecological Applications, in review.
Kotanen, P.M. 1997. Effects of experimental soil disturbance on revegetation by natives and exotics in coastal Californian meadows. Journal of Applied Ecology 34: 631-644.
Incerti, M., P.F. Clinnick, and S.T. Willatt. 1987. Changes in the physical properties of a forest soil following logging. Australian Forest Research 17: 91-98.
Lynch, D., W.H. Romme, and M.L. Floyd, 2000. Forest restoration in southwest ponderosa pine. Journal of Forestry 98: 17-24
Malmer, A. and H. Grip. 1990. Soil disturbance and loss of infiltrability caused by mechanized and manual extraction of tropical rainforest in Sabah, Malaysia. Forest Ecology and Management 38: 1-12.
McClune, B. and M.J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, Oregon, USA.
McNabb, D.H., A.D. Startsev, and H. Nguyen. 2001. Soil wetness and traffic level effects on bulk density and air-filled porosity of compacted boreal forest soils. Soil Science Society of America Journal 65: 1238-1247.
Milliken, G.A., and D.E. Johnson. 1984. Analysis of messy data, Vol. I. Designed experiments. Van Nostrand Reinhold Co., New York.
Moore, M.M., W.W. Covington, and P.Z. Fulé. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. Ecological Applications 9: 1266-1277.
Page-Dumbroese, D.S., M.F. Jurgensen, R.E. Brown, and G.D. Mroz. 1999. Comparison of methods for determining bulk densities of rocky forest soils. Soil Science Society of America Journal 63: 379-383.
Rab, M.A. 1994. Changes in physical properties of a soil associated with logging of Eucalyptus regnans forest in southeastern Australia. Forest Ecology and Management 70: 215-229.
Rab, M.A. 1996. Soil physical and hydrological properties following logging and slash burning in the Eucalyptus regnans forest of southeastern Australia. Forest Ecology and Management 84: 159-176.
Stylinkski, C.D., and E.B. Allen. 1999. Lack of native species recovery following severe exotic disturbance in southern Californian shrublands. Journal of Applied Ecology 36: 544-554.
Terrestrial Ecosystems Survey of the Coconino National Forests. 1995. U.S. Department of Agriculture, Forest Service, Southwest Region.
Wali, M.K. 1999. Ecological succession and the rehabilitation of disturbed terrestrial ecosystems. Plant and Soil 213: 195-220.
Zar, J.H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall. Englewood Cliffs, New

Jersey, USA.

Table 1. Soil bulk density of clay loam forest soils to 4.8 cm depth in areas thinned with different thinning intensities and different harvest systems.

Thinning	Mean Bulk Density ($g\ cm^{-3}$)	SEM (+/-)	Change from undisturbed site (%)
Control	1.038	0.041	0
Low Intensity	1.167	0.015	11.06
Intermediate Intensity	1.122	0.016	7.49
High Intensity	1.133	0.037	8.39
Machine System	1.165	0.012	n/a
Hand System	1.096	0.023	n/a
Whole-Tree System	1.169	0.015	n/a

*There were no significant differences among thinning intensities or among harvest systems.

Table 2. Dead woody biomass of pre-existing and harvest material and forest floor depth for areas thinned with different thinning intensities and harvest systems, prior to prescribed burning. Data are presented as mean ± SEM (standard error of the mean), N=3.

Thinning	Total Woody Fuels (kg/hectare)	Total Forest Floor Depth (cm)
Control	59.33 (10.39) **a**	5.41 (0.31) **a**
Low Intensity	48.16 (5.47) **a**	5.59 (0.66) **a**
Intermediate Intensity	58.64 (10.16) **a**	5.18 (0.56) **a**
High Intensity	61.98 (10.59) **a**	5.23 (0.48) **a**
Machine System	63.16 (11.16) **a**	5.16 (0.74) **a**
Hand System	66.69 (9.59) **a**	5.64 (0.41) **a**
Whole-Tree System	38.94 (5.46) **b**	5.13 (0.33) **a**

*Values followed by different letters are significantly different at the 0.05 level between the different thinning intensities and between the different harvest systems.

Table 3. Trees/hectare, basal area, and tree canopy cover with different thinning intensities and harvest systems for pretreatment (1998) and post-treatment (2000) data. Data are presented as mean ± SEM (standard error of the mean), N=3.

Thinning	Trees/hectare		Basal area (m^2/ha)		Tree canopy cover (%)	
	Pre	Post	Pre	Post	Pre	Post
Control	1187.52 (307.07) **a**	1186.2 (306.1) **a**	37.72 (1.92) **a**	37.71 (1.93) **a**	64.9 (5.4) **a**	61.8 (4.6) **a**
Low Intensity	955.43 (110.47) **a**	140.42 (27.03) **b**	34.09 (1.71) **a**	22.31 (0.84) **b**	58.9 (5.3) **a**	40.0 (2.9) **b**
Intermediate Intensity	1492.1 (344.43) **a**	170.0 (12.14) **b**	38.49 (1.03) **a**	17.85 (3.56) **b**	64.2 (3.7) **a**	32.0 (2.9) **b**
High Intensity	1043.35 (442.69) **a**	242.92 (31.95) **b**	34.79 (2.45) **a**	15.56 (3.64) **b**	56.7 (3.9) **a**	29.7 (5.0) **b**
Machine System	1185.85 (412.81) **a**	186.25 (6.42) **b**	33.61 (1.62) **a**	22.61 (1.06) **b**	51.6 (2.6) **a**	39.4 (2.9) **b**
Hand System	1578.35 (219.24) **a**	213.34 (47.09) **b**	36.80 (2.28) **a**	19.54 (1.28) **b**	63.0 (3.2) **a**	35.4 (3.0) **b**
Whole-Tree System	726.67 (97.35) **a**	154.75 (39.15) **b**	36.98 (2.05) **a**	13.57 (3.81) **b**	65.0 (1.0) **a**	27.5 (4.0) **b**

*Values followed by different letters are significantly different at the 0.05 level between pretreatment and post-treatment values for an individual variable within one thinning treatment. There were no statistical differences between treatment intensities or between harvest systems for any of the variables for pretreatment or post-treatment data.

Table 4. Percentage of non-native species for areas thinned with different thinning intensities and harvest systems for pretreatment (1998), post 1 (1999), post 2 (2000) and post 3 (2001) data. Data are presented as mean ± SEM (standard error of the mean), N=3.

Thinning	1998	1999	2000	2001
Control	0.62 (0.2) **a**	0 (0) **a**	0.17 (0.17) **a**	0.12 (0.12) **a**
Low Intensity	0.7 (0.1) **a**	0.42 (1.65) **a**	1.29 (4.54) **a**	1.72 (5.02) **a**
Intermediate Intensity	0.55 (0.16) **a**	1.22 (0.95) **a**	4.45 (2.86) **a**	9.64 (6.87) **a**
High Intensity	0.1 (0.07) **a**	1.86 (0.21) **a**	4.71 (1.17) **a**	5.13 (1.08) **a**
Machine System	0.38 (0.24) **a**	0.54 (0.05) **a**	1.06 (0.78) **a**	1.72 (0.96) **a**
Hand Technique	**0.18** (0.18) a	**0** (0) a	**0.23** (0.23) a	**0.69** (0.69) a
Whole-Tree Technique	0.16 (0.08) **a**	2.95 (1.3) **b**	9.16 (2.97) **c**	14.1 (5.69) **c**

*Values followed by different letters are significantly different at the 0.05 level across time for individual thinning intensities and harvest systems.

Figure Headings

Figure 1. Study site map near Flagstaff, Arizona. There are three blocks with four treatment units. Control units (no thinning or burning) are represented by a _-1, low intensity units (thinning to a high level of remaining trees) are represented by a _-6, intermediate intensity units (thinning to an intermediate level of remaining trees) are represented by a -5, and high intensity units (thinning to a low level of remaining trees more similar to the forest density prior to settlement) are represented by a -2.

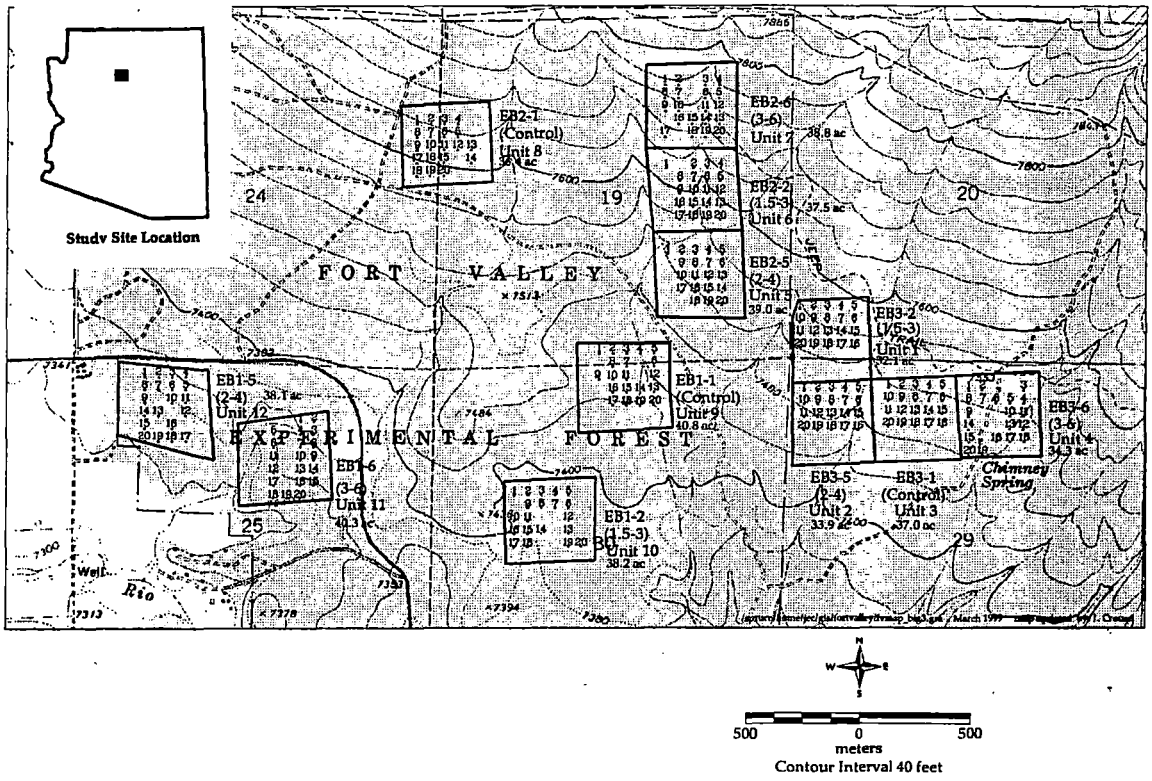
Figure 2(a-b). a) Example of a stand thinned using the hand system. Tape in center of the photograph is where soil profile disturbance, fuel loads, and vegetation response were measured; and b). example of heavy soil disturbance (area where more than 75% of the O-horizon has been removed or disturbed and/or where deep gouges or ruts are visible in the mineral soil).

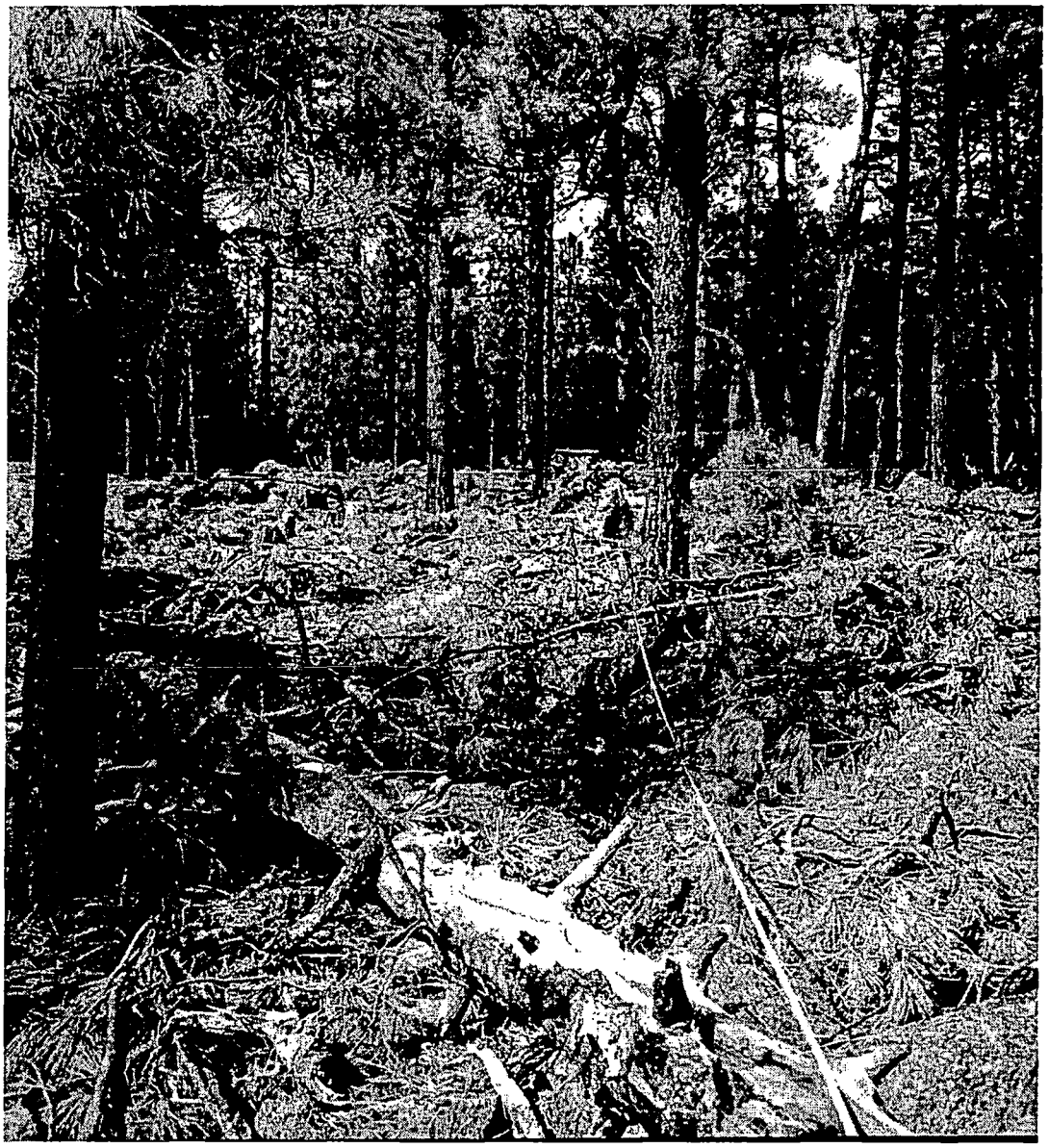
Figure 3 (a-c). The percent of soil profile disturbance broken into different categories: no disturbance, low disturbance, intermediate disturbance, high disturbance, and bladed road for a) three different thinning intensities; b) three different harvest systems; and c) pre and post slash piling. Significant differences between the various treatments within individual soil disturbance categories were determined by ANOVA and are denoted by asterisks.

Figure 4 (a-b). Ordinations of plant community data for pretreatment (1998) and post-treatment (2001) data determined with non-metric multidimensional scaling (NMDS) for a) three different thinning intensities and controls, and b) three different harvest systems and controls. Each symbol represents the plant community for a specific unit and year (pre or post). Plant communities that are more similar are found closer together and plant

communities that are more dissimilar are further apart. Plant community data were relativized to the maximum value prior to analysis to omit noise caused by very rare species. NMDS scree plots were examined to select the appropriate dimensionality in NMDS analysis. Joint plot vectors show the relationship between community variables and the herbaceous plant community. The angle and length of the line indicate the direction and strength of the relationship.

Fort Valley Study Site
Ponderosa Pine Ecosystem Restoration
Coconino National Forest





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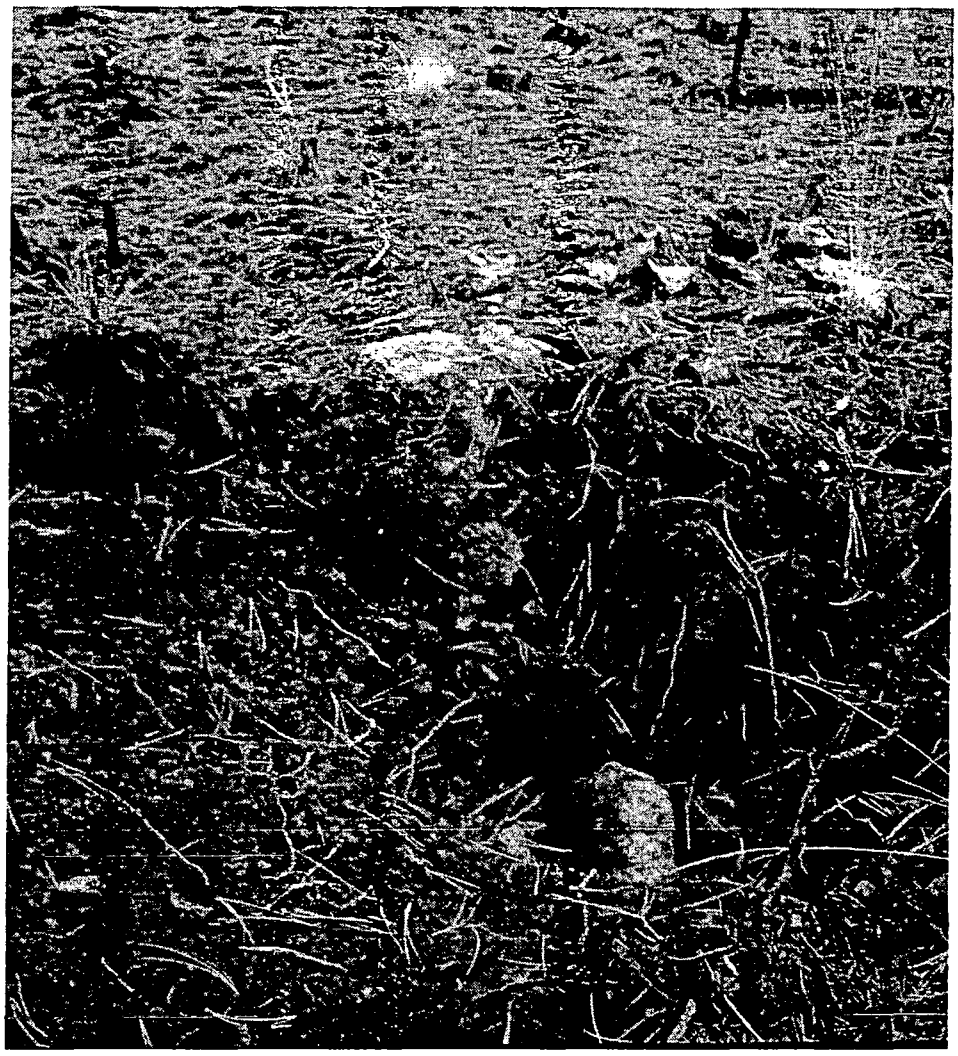

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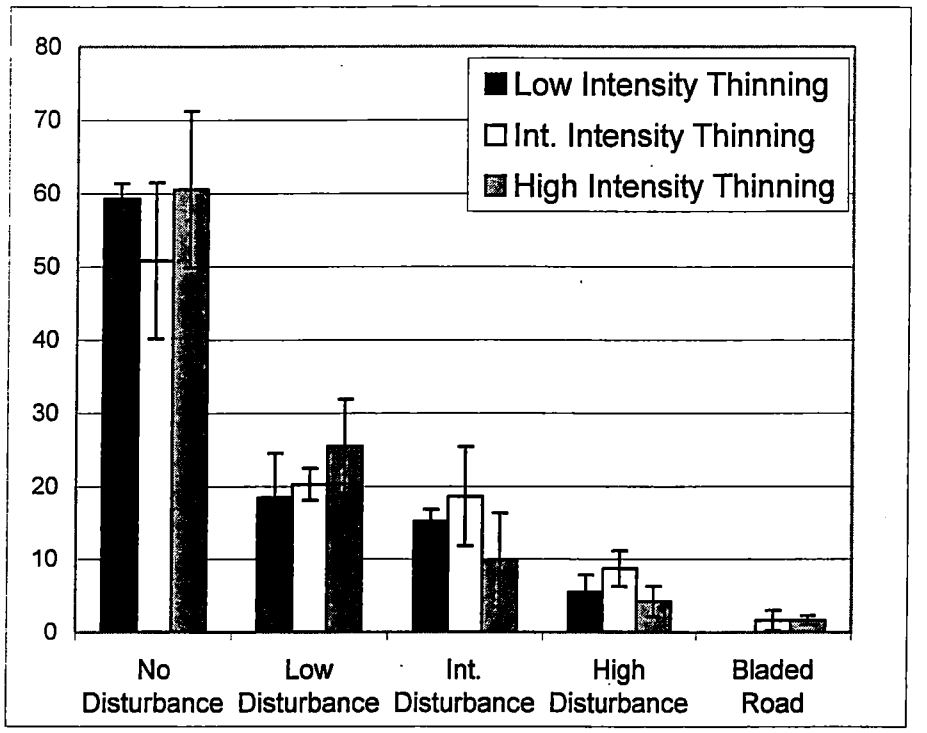


Figure 3a.

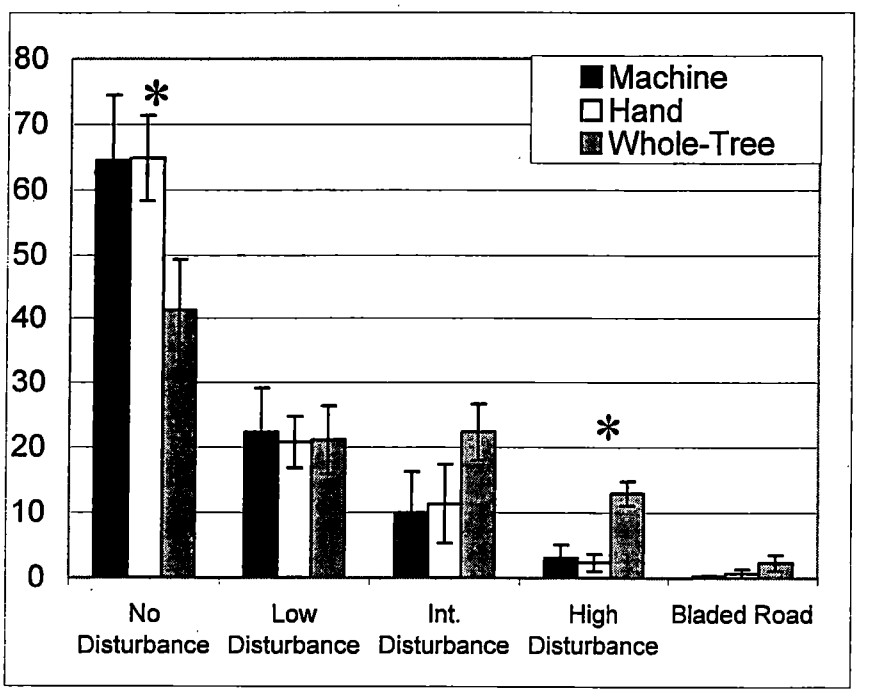


Figure 3b.

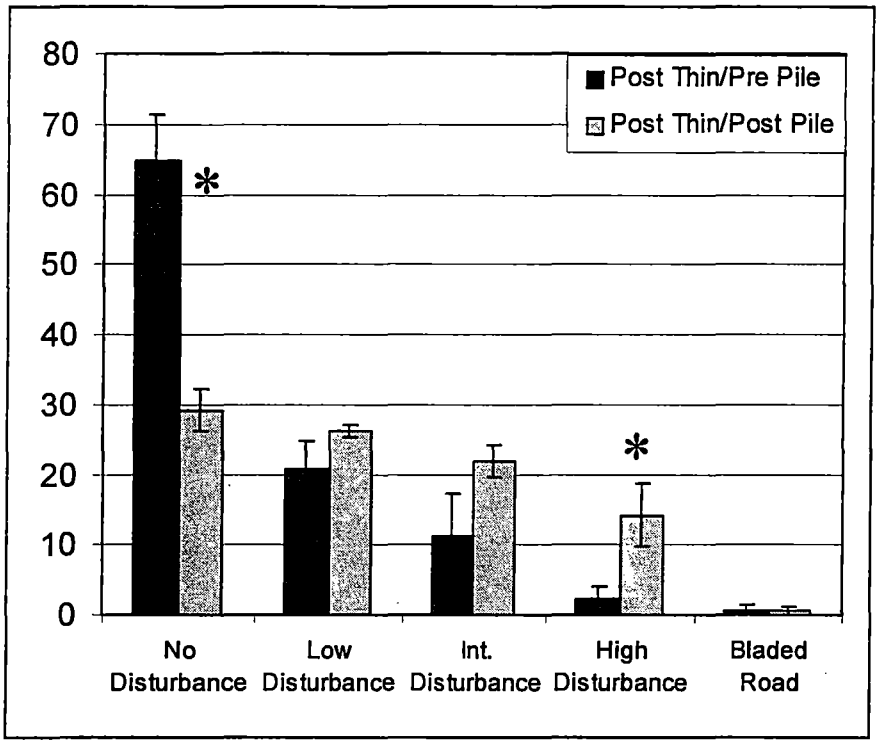
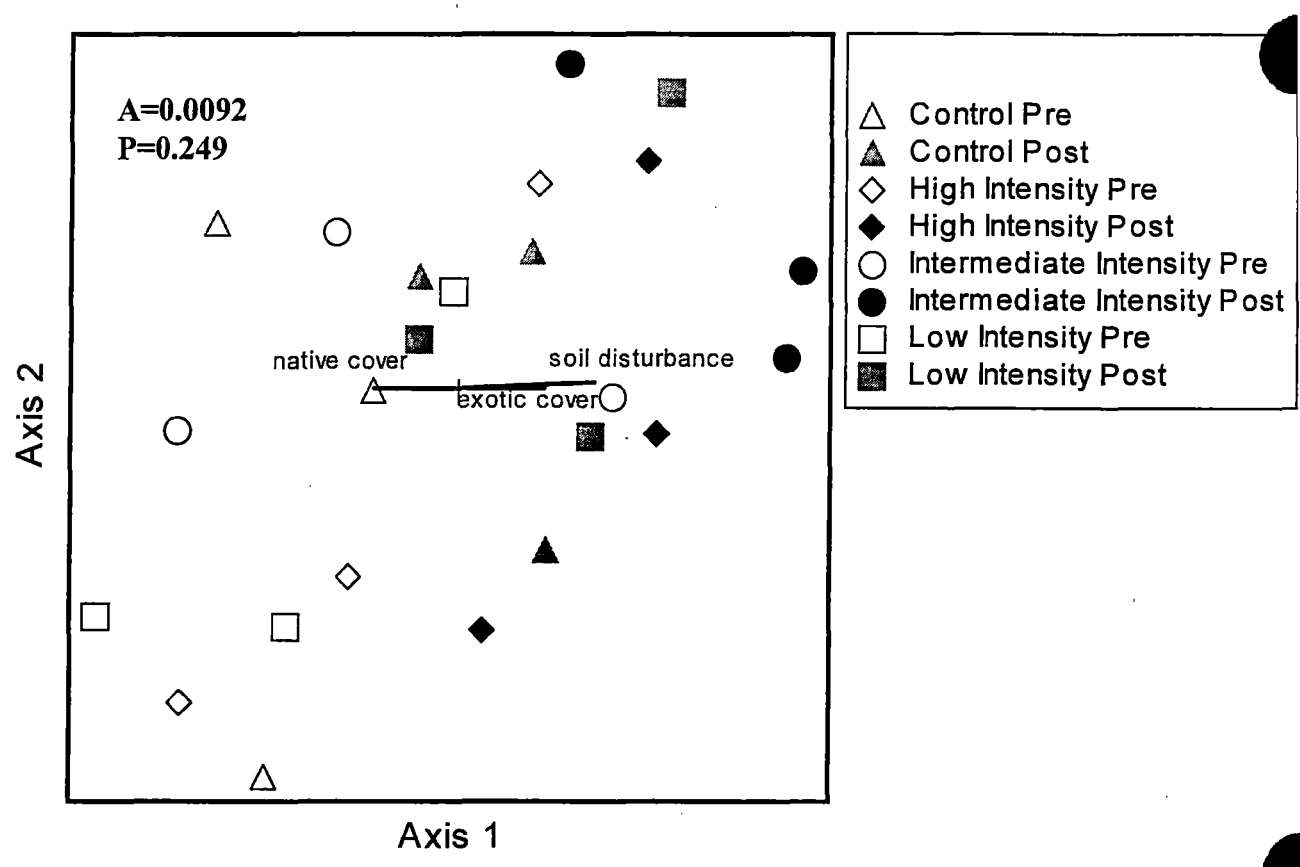

80
70
60
50
40
30
20
10
0
Post Thin/Pre Pile
Post Thin/Post Pile
*
*
No Disturbance
Low Disturbance
Int. Disturbance
High Disturbance
Bladed Road

Figure 3c.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soil disturbance
exotic cover
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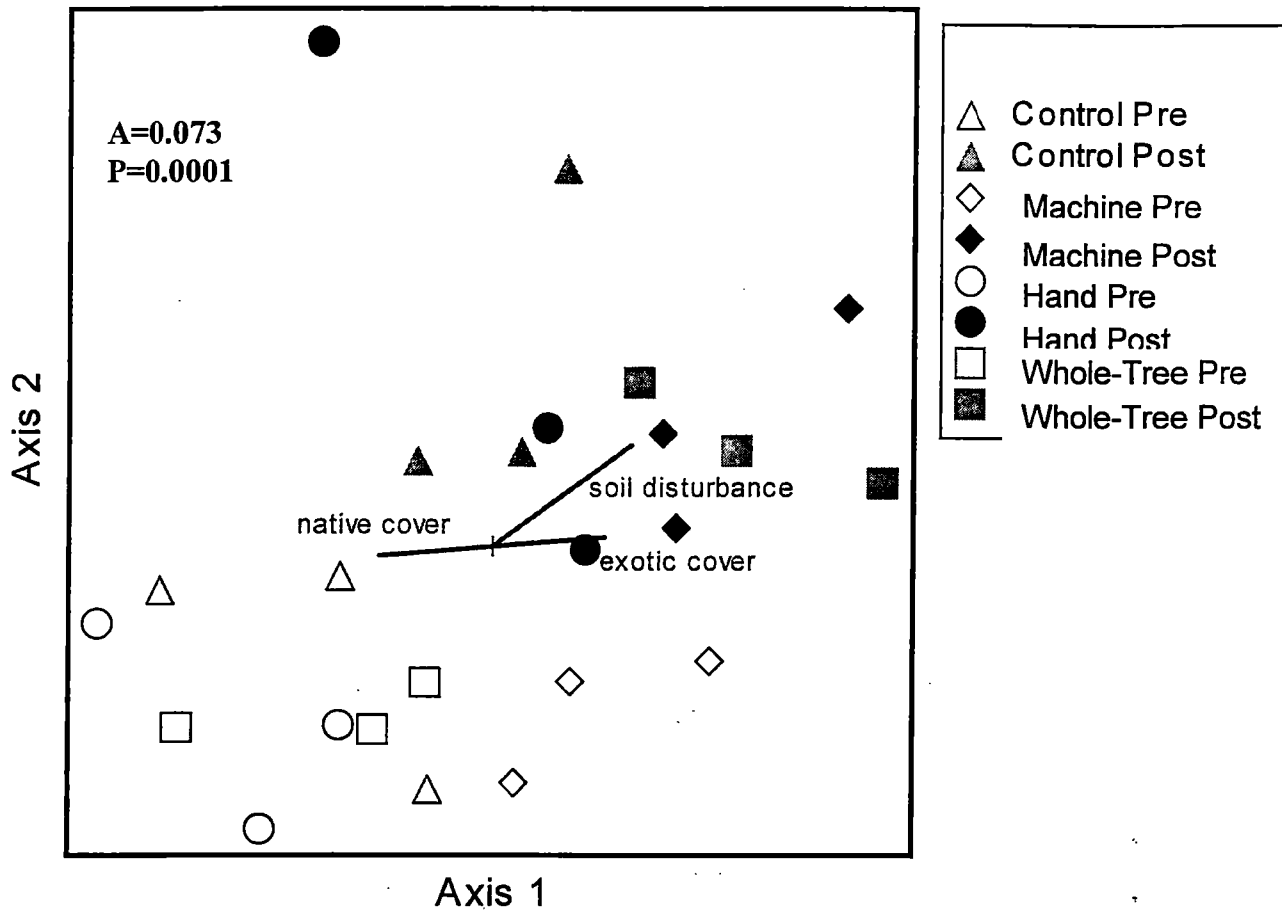
Intermediate Intensity Post
Low Intensity Pre
Low Intensity Post

Figure 4a.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Axis 1
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soil disturbance
exotic cover
Control Pre
Control Post
Machine Pre
Machine Post
Hand Pre
Hand Post
Whole-Tree Pre
Whole-Tree Post

Figure 4b.

A Rapid, Non-destructive Sampling Technique for Estimating Plant Biomass in Large-Scale Ecological Restoration Treatments

Restorationists use many different plant attributes to quantify the response of vegetation to ecological restoration treatments, such as fecundity, growth rate and cover. Plant biomass is one attribute that is preferred over others because it provides information on site productivity, potential fire behavior, and responses to restoration. However, plant biomass is often not quantified in restoration treatments because it can be destructive, expensive and time-consuming. Researchers have developed numerous techniques to estimate plant biomass and overcome these obstacles. The sampling technique used for determining plant biomass should be based upon: 1) the size of the study area; 2) desired accuracy; 3) structure of the vegetation; and 4) vegetation of interest (Catchpole and Wheeler, 1992).

In the summer of 1998, a cooperative working group of researchers, scientists, and interested community members implemented a large-scale ponderosa pine (*Pinus ponderosa*) forest restoration project near Flagstaff, Arizona. Prior to the mid-1880's, ponderosa pine ecosystems in the Southwest were characterized by large, old-growth trees, a frequent, low intensity fire regime, and a diverse, productive herbaceous understory (Covington *et al.* 1997). Land use changes around the turn of the 20th century, including old-growth tree harvesting, cattle and sheep grazing, and active fire suppression, provided the conditions for the establishment of numerous trees that outcompeted the herbaceous understory vegetation. The primary goals of this project were to reduce the risk of large high-mortality crown fires and to restore the structure and function of the system within the range of natural variability. Enhancing the herbaceous understory is a major component to accomplishing this goal. Therefore a method for quantifying plant biomass is desirable to measure the herbaceous plant response.

We combined two sampling techniques to estimate plant biomass in large-scale restoration treatments in southwestern ponderosa pine forests: the photo guide technique and the comparative yield technique (Freidel and Bastin, 1988). The photo guide technique entails the creation of several photo keys of different biomass levels from destructive biomass sampling for different vegetation types. For our photo guide, we chose three different vegetation types based upon the extant vegetation in the restoration treatments: a graminoid-dominated vegetation type (grass-like plants), a forb-dominated vegetation type, and a mixed graminoid/forb-dominated vegetation type (Figure 1). For each vegetation type we photographed and clipped ten different levels of biomass ranging from 10 kg/ha to 1640 kg/ha in 1m^2 (0.5m X 2.0m) plots, the same size plots we used for estimating biomass. We then chose seven of the ten plots to use in our photo guide to create a series of different levels of biomass that increased from low to high plant biomass. In each plot, we identified all species, estimated their aerial cover visually, and measured their average height. This information was then tabulated in the photo guide series so that individual species' biomass could be estimated within the plots and so species could be distinguished in the photographs. We determined actual plant biomass for individual species in the plots by drying the clipped samples for 24 hours in an oven at 70° C and weighing the plants to within 0.01 gram. We then used our photo guide to implement the comparative yield technique, which involves estimating plant biomass weight from reference standards.

The cooperative working group established three replicate blocks of four different treatments of approximately 50 acres each. The four treatments consisted of: 1) thinning to a low level of replacement trees and burning; 2) thinning to an intermediate level of replacement trees and burning; 3) thinning to a high level of replacement trees and burning; and 4) no thinning or burning. We established twenty 50m transects on a systematic grid within each treatment unit. Along each transect, we established four $1m^2$ plots at 10m, 20m, 30m, and 40m on alternate sides of the transect. Using the photo guide we developed, we estimated forb and graminoid biomass separately for each $1\text{-}m^2$ plot, for a total of 80 plots per treatment unit. Specifically, we used three steps to estimate overall biomass. The first step we used was to classify the plot into one of the three vegetation types: a graminoid-dominated vegetation type, a forb-dominated vegetation type, or a graminoid/forb-dominated vegetation type. Next we classified the plot into one of the seven biomass levels within the vegetation type chosen in step one and estimated the weight of each individual species based upon its aerial cover and height, as compared to the cover, height and corresponding weight values of actual plant species in the photo guide series. When a particular species was not found in the photo guide series, we estimated biomass values based on a species that had a similar vegetation structure. We then grouped individual species into graminoid and forb functional groups and summed the biomass values for the individual species to obtain a total value for each functional group. We randomly selected eight of the twenty transects in each unit to double-sample, and clipped the plots located at 20m along the transect, separating the biomass into forb and graminoid classes.

We used linear regression analysis to determine the relationship between actual and estimated plant biomass, transforming data when necessary to meet the variance assumptions for regression analysis. We found a high correlation between actual and estimated biomass for both forbs (r^2=0.87, p=<0.0001; y=0.19433 + 0.88694x) and graminoids (r^2=0.89, p=<0.0001; y=0.1942 + 0.82869x). These results indicate that the comparative yield sampling technique combined with a photo guide can be used as an alternative to destructive biomass sampling in large-scale restoration treatments in the Southwest. On average, estimating biomass plots was three times faster than clipping biomass plots. We believe that the decrease in the relative cost of biomass sampling along with the reduction in destructive sampling will, in many cases, outweigh the minimal loss of accuracy for our plant biomass estimates in this study. Sampling all 960 $1m^2$ plots used in this study was unrealistic due to financial restraints, and undesirable because of the removal of aboveground plant biomass. We endorse this combined biomass sampling technique for other large-scale restoration studies where quantifying plant biomass is desired and money and time are limited. In addition, we recommend that this technique should be developed using species that are common in the study area and representative of common vegetative structural forms (e.g., tall and slender forbs, dense mat forbs, bunchgrasses, etc.) to increase the accuracy of the biomass estimates. We also recommend that the number of researchers estimating biomass should be kept to a minimum to reduce variation between estimators. In our study, we used three field researchers to estimate plant biomass. Finally, all estimators should practice double-sampling before using the photo guide in the field, and throughout the duration of the experiment to determine and maintain their accuracy in estimating plant biomass, i.e., whether they tend to over- or under-estimate plant biomass.

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References

Catchpole W.R. and C. J. Wheeler 1992. Estimating plant biomass: a review of techniques. *Australian Journal of Ecology* 17: 121-131.

Covington W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. *Journal of Forestry* 95: 23-29.

Freidel, M. H. and G. N. Bastin 1988. Photographic standards for estimating comparative yield in arid rangelands. *Australian Rangeland Journal* 10: 34-38.

Part TWO:

Publications from RMRS-99156-RJVA

Peer-reviewed Publications

Korb, J.E., N.C. Johnson, and W. W. Covington. 2001. Preliminary results-The effects of restoration thinning on mycorrhizal fungal propagules in a northern Arizona ponderosa pine forest. In: Vance, G.K., W.W. Covington, and C.B. Edminster (compilers), Ponderosa Pine Ecosystems Restoration and Conservation: Steps Toward Stewardship. Proc. RMRS-P-22. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Korb, J.E. and J.D. Springer. 2002. Invited book chapter: Herbaceous understory response to ponderosa pine restoration thinning and prescribed burning. In: Ecological Restoration of Southwestern Ponderosa Pine Forests. Island Press, Washington, D.C.

Korb, J.E. and J.D. Springer. 2002. Technique for estimating plant biomass reduces destruction, cost, and sampling time. Ecological Restoration 19(5): in press.

Korb, J.E., N.C. Johnson and W.W. Covington. Arbuscular mycorrhizal propagule densities respond rapidly to thinning and prescribed burning in two southwestern ponderosa pine restoration treatments. Journal of Applied Ecology, in press.

Submitted

Korb, J.E., W.W. Covington, and P.Z. Fulé. Choosing the appropriate sampling technique to detect change-- An example from ponderosa pine restoration. Submitted to Restoration Ecology, accepted.

Korb, J.E., N.C. Johnson, and W.W. Covington. Slash pile burning affects on mycorrhizae, soil properties, and plant establishment: recommendations for amelioration. Submitted to the Ecology Letters, in review.

Korb, J.E., B. Gideon, and P.Z. Fulé. Soil disturbance and herbaceous response associated with different harvest systems and intensities. Submitted to Forest Science, in review.

In Preparation

Korb, J.E., Springer, J.D., Power, S., and M.M. Moore. The role of the soil seed bank in Ponderosa pine restoration. To be submitted to the Canadian Journal of Botany.

Korb, J.E., P.Z. Fulé, Springer, J.D., and W.W. Covington. Land-use history influences herbaceous understory successional trajectories following ponderosa pine restoration. To be submitted to Journal of Ecology, in preparation.

Presentations from RMRS-99156-RJVA

Oral Presentations

Korb, J.E. 2002. Invited symposium speaker. Adaptive management experimentation in ponderosa pine forest restoration. Ecological Society of America and Society of Ecological Restoration joint annual meeting. Tuscon, Arizona.

Korb, J.E., J.D. Springer, W.W. Covington, and P.Z. Fulé. 2001. Is your vegetation sampling design influencing your results? —An example from ponderosa pine restoration. 6th Biennial Colorado Plateau Conference. Flagstaff, Arizona.

Korb, J.E., N.C. Johnson, and W. W. Covington. 2001. Mycorrhizal fungal responses to ponderosa pine restoration thinning and prescribed burning treatments. Ecological Society of America annual meeting. Madison, Wisconsin.

Korb, J.E., N.C. Johnson, and W.W. Covington. 2001. The effects of slash pile burning on AM propagule densities and seedling emergence. Society for Ecological Restoration Colorado Rockies Chapter annual meeting. Keystone, Colorado.

Korb, J.E., W.W. Covington, and P.Z. Fulé. 2000. The role of the soil seed bank in ponderosa pine restoration. Ecological Society of America annual meeting. Snowbird, Utah.

Poster Presentations

Korb, J.E., N.C. Johnson, and W. W. Covington. 2001. Slash pile burning significantly reduces arbuscular mycorrhizal propagule densities and the soil seed bank. Putting the Pieces Together: Practicing Forest Ecosystem Restoration Conference. Flagstaff, Arizona.

Korb, J.E., N.C. Johnson, and W. W. Covington. 2000. The effect of restoration thinning on mycorrhizal fungal propagules in a northern Arizona ponderosa pine forest. Steps Toward Stewardship-Ponderosa Pine Ecosystems Restoration and Conservation Conference. Flagstaff, Arizona.

Korb, J.E., W.W. Covington, and P.Z. Fulé. 1999. Buried propagule bank of thinned and unthinned ponderosa pine stands in northern Arizona. 5th Biennial Colorado Plateau Conference. Flagstaff, Arizona.